Population Ecology of the Polynesian Rat, *Rattus exulans*, on Kure Atoll, Hawaii[1]

WILLIAM O. WIRTZ II[2]

ABSTRACT: A population of the Polynesian rat, *Rattus exulans,* was studied at Green Island, Kure Atoll, in the northwestern Hawaiian Islands from September 1963 through August 1965. The island covers 214 acres, of which 144 are vegetated, and all vegetated areas are utilized by the rat. Other vertebrates on the island and its shores include 14 species of breeding seabirds and the Hawaiian monk seal. Usual predators of rodents are absent and seasonal climatic fluctuations are slight. Juveniles are weaned and leave the nest at 2 to 3 weeks. A prolonged maturational molt occurs between the ages of 4 and 9 weeks. Most young, or nonbreeding, adults overwinter before attaining sexual maturity. Once sexual maturity is attained males remain fertile throughout the year. Reproduction is seasonal, most litters being produced from May through August and none from September through December. Mean litter size is four, and usually only one litter is produced per female per year for a mean of 4.77 young per mature female annually. About 360 young were produced on a 6.94-acre study area in one breeding season. The only ectoparasites recorded are the louse *Hoplopleura pacifica* and the mites *Laelaps nuttalli* and *L. echidninus.* Approximately 62 percent of the diet on Kure is composed of plant material, 30 percent of insects, and 8 percent of vertebrate flesh. Breeding males move significantly greater distances between captures and have significantly larger home ranges than breeding females. The size of the home range of breeding adults is not affected by density fluctuations or reproductive activity. Mean population density for the period studied is 45 rats per acre, or 6,480 individuals for the entire island, and density fluctuated from lows of 30 per acre in March of both years to a high of 75 per acre, about 10,800 on the island, in September 1964. Mean adrenal weight in subadult and adult animals is correlated with density, and also with reproductive activity in breeding adults. Mean body weight and extent of subcutaneous and mesenteric fat deposits are significantly reduced during the winter.

Seasonal reproduction results in high population densities by early winter. Sharp declines in density are observed during the winter and early summer, in association with increased mean adrenal gland weight in early winter and decreased mean body weight and fat deposition in late winter and early summer. Because of the absence of predators and the apparent absence of epidemic disease it is suggested that population regulation is achieved chiefly through the interaction of density with available food resources; and with that portion of the population which cannot obtain sufficient food and/or shelter being eliminated during the winter to reduce numbers to a favorable balance with resources by early summer, at which time reproduction is again initiated among the surviving individuals.

THE POLYNESIAN RAT, *Rattus exulans* (Peale), is widely distributed over most of the islands of the central and western Pacific from the Asiatic mainland and New Guinea east to the Hawaiian Islands and Easter Island, and south to the Kermadecs and New Zealand. Races of the species are now known from most major island chains and many isolated islands within the region (Ellerman, 1941).

The arrival of rodents in the Hawaiian Is-

[1] Pacific Ocean Biological Survey Program Contribution no. 62. Manuscript received 20 March 1972.

[2] Department of Zoology, Pomona College, Claremont, California 91711.

lands does not appear to be documented, though tradition and early accounts of the Hawaiians indicate that a native rat was present and known to them as *iole* (Bryan, 1915). This rat, pigs, and dogs, animals usually associated with Polynesian cultures (Tomich, 1969), were the only terrestrial mammals native to the Hawaiian Islands at the time of their discovery by Captain Cook in 1778. The subsequent introduction of *Rattus rattus* and *R. norvegicus* by European colonists and the introduction of the mongoose, *Herpestes auropunctatus,* from Jamaica in 1883 (Bryan, 1915) may have led to rapid decimation of the native species. The first scientific records of a native rat remaining in the Hawaiian Islands are those of Stone (1917) and Stokes (1917).

The presence of rodents on Kure Atoll, 1,175 miles northwest of the main Hawaiian Islands, was noted in 1870 by the crew of the U.S.S. *Saginaw* (Read, 1912), and again in 1915 by the crew of the cutter *Thetis* (Munter, 1915).

Rattus rattus and *Mus musculus* occur today on Midway Island, 57 miles east of Kure, the house mice having been introduced early in the history of human utilization of that island and the rat having apparently been introduced in 1942 or 1943 (Johnson, 1945). No terrestrial mammals occur on any of the five uninhabited islands between Kure and Midway and the main islands, though there is a questionable record of mice occurring on Lisianski Island in the 1890s (Cameron and Farrell, 1928). Trapping and surveys on this island from 1963 through 1965 produced no evidence that any rodents exist there today.

An intensive investigation of the population ecology of *Rattus exulans* on Kure Atoll was begun in October 1963 and continued through August 1965. Principal objectives of this study were to collect information on population dynamics and reproductive biology of the species on Kure for comparison with data available for other populations and to investigate the interactions of the rat with the nesting seabirds utilizing the island. In a broader context, the study offered a unique opportunity to examine in detail the mechanisms of population regulation of a single mammalian speices in a simplified oceanic island ecosystem.

DESCRIPTION OF THE STUDY AREA

Topography

Kure is a low coral atoll at the northwestern end of the Hawaiian Archipelago (lat 28°25′ N, long 178°10′ W) approximately 1,175 miles northwest of Honolulu. The atoll has a nearly circular fringing reef that is approximately 15 miles in circumference and 5 miles at its greatest diameter. The only permanent landmass within the reef is 214-acre Green Island, located about one-fourth of a mile from the reef in the southeast section of the lagoon. It is 1.43 miles in greatest length and 0.37 mile in maximum width. Most of the island is covered by dense growth of beach magnolia, *Scaevola taccada,* except for a low depression in the northern half known as the central plain. Modification of the island from the construction of a Coast Guard station in 1961 has reduced the vegetated area to approximately 144 acres, including the central plain of about 15 acres.

Soils on Green Island range from pure sand and coralline gravel on the beaches to humus-sand mixtures in heavily vegetated areas and around seabird rookeries. The beaches along the eastern and southern sides of the island are moderately sloping, from 50 to 100 ft wide, and strewn with small stones and pebbles, especially along the southern side. At the northern and western ends of the island are fluctuating sand points that may extend for 500 yards or more. The beaches along the inner or lagoon side of the island are wider, up to 200 ft in places, gently sloping, and composed chiefly of fine sand. Maximum elevations for the island occur in a line of dunes along the inner beach which range in height from 20 to 25 ft above sea level. Dunes along the northeastern and southern beaches range from 8 to 15 ft, those in the southwestern interior range from 6 to 16 ft in elevation, and the entire central plain is only 6 to 8 ft above sea level. Man-made features on the island include buildings, water and fuel tanks, recreation areas, lawns, roads, a runway, and a 625-foot antenna with an extensive system of moorings, guy wires, and ground wires. Though paths and roads were cut in the vegetation during the construction of these facilities, growth in the ensuing years has almost obliterated the scars. The 4,000-foot runway

runs in a northeast–southwest direction along the south side of the southwestern half of the island.

There is no natural standing water on the island, though the roads and runway catch water and hold it for short periods after heavy rains.

Climate

The climate of this region of the Pacific is marine and is influenced by marine tropical or marine Pacific air masses, depending upon the season. During the summer the region is under the influence of easterlies with marine tropical and trade winds prevailing. Winter weather is more variable due to an interplay between the Aleutian Low and the Pacific High.

Mean monthly temperature and range of mean daily temperature for each month are given in Fig. 1. During this study mean monthly temperatures ranged between 62° F and 66° F from December through April and between 67° F and 81° F from May through November. Mean monthly relative humidity varied between 80 and 90 percent. Though both temperature and relative humidity were high from June through October there is no apparent correlation between the equally high relative humidity observed during other months and reduced mean temperature. Both monthly precipitation and number of days with measurable precipitation were extremely variable, and increased monthly precipitation was correlated with the occurrence of single heavy storms during the month. Precipitation was most prevalent from November through January and least prevalent from April through June. Precipitation was more frequent from November through March, though monthly totals were similar, and individual heavy falls occurred from April through July and from October through December. Rapid percolation through the highly porous coral soils may preclude effective utilization of heavy showers by the vegetation. Measurable precipitation frequently fell on days that were not predominantly cloudy, and overcast days did not necessarily bring precipitation. As with the data on rainfall, the data on overcast conditions show little correlation between years.

Winds were lowest in May and June and highest in March and December. They occurred

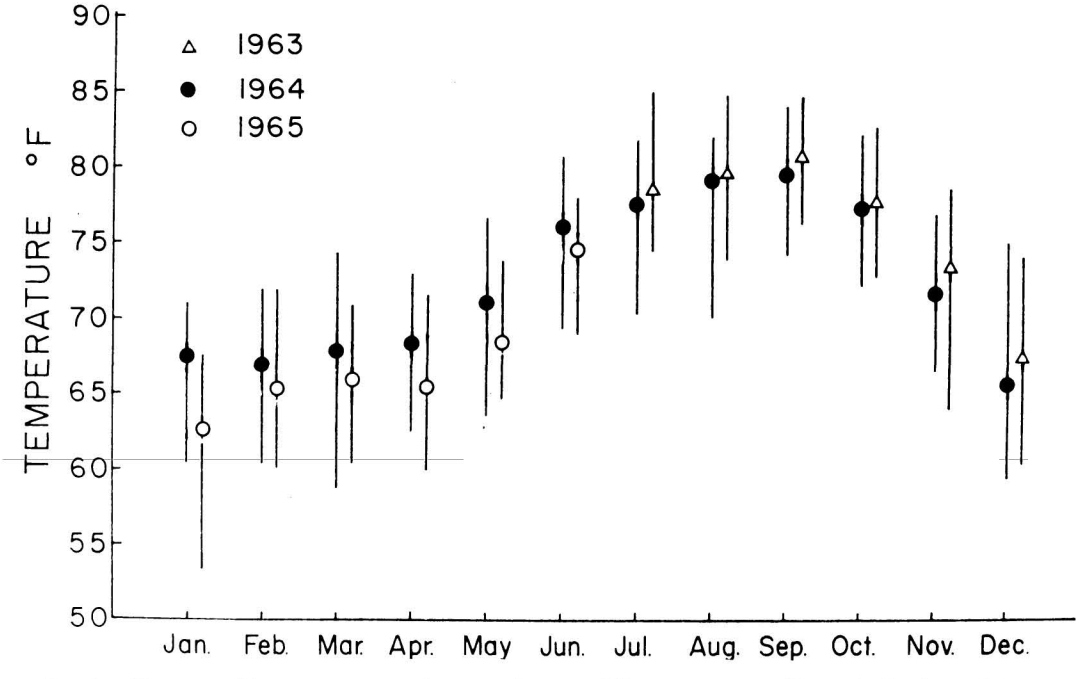


FIG. 1. Mean monthly temperature and range of mean daily temperature, Kure Atoll, from July 1963 through June 1965.

most frequently from the east or northeast from March through November, though they were quite variable in June; from the west in December; and from the southwest to south in January and February. Peak gusts of 77 and 67 knots were recorded in December and January, respectively, during the period when the easterlies were not present.

Blumenstock and Price (1967) generalized about the weather of the Hawaiian region, and concluded that there is a 7-month winter from October through April and a 5-month summer from May through September, with no spring or fall. Fig. 1 suggests that winter at Kure is December through April; and summer, May through November.

Vegetation

The native vascular flora of Green Island consists of 13 species representing 12 genera and 10 families (Clay, 1961; Lamoureux, 1961). An additional four genera representing three additional families should probably be included in the native flora, though they were not reported by Christophersen and Caum (1931) who conducted a botanical survey of the island in April 1923. Increased human utilization of the island dating from World War II and culminating in the construction of the Coast Guard facility in 1961 has resulted in the addition to the flora of 24 exotic species representing eight different families. Ten of these species are ornamental plantings around buildings, but the remainder are considered to be accidental introductions (Clay, 1961; Lamoureux, 1961).

Ten native species are of significance to the ecology of the island. A major portion of the island, except for small clearings and the central plain, is covered by *Scaevola taccada*, a scrubby xerophyllous bush of dense gnarled growth form which occasionally reaches heights of 8 feet and which is presumed to be a major factor in modifying the effects of wind, rain, and insolation on the terrestrial microenvironment. Small open areas in the *Scaevola* support growth of the bunchgrass *Eragrostis variabilis* and the herbaceous vine *Boerhavia diffusa.* Less abundant in these clearings are a second herbaceous vine, *Tribulus cistoides,* and a woody vine, *Solanum nelsoni.* All three vines, and especially *Boerhavia* and *Solanum*, sometimes spread beneath stands of *Scaevola* which are not so dense as to exclude sunlight. Exposed dunes at the periphery of the island support *Eragrostis variabilis* and the related *E. whitneyi,* in addition to *Boerhavia.*

Additional species are found only on the central plain. A native morning glory, *Ipomoea indica,* is extremely abundant at the southern end of the plain, where it has grown into and over adjacent *Scaevola* growth. A crucifer, *Lepidium o-waihiense*; a cucurbit, *Sicyos hispidus*; and the only native composite, *Lipochaeta integrifolia*; occur chiefly in the central plain. All three are common, and the crucifier and composite move rapidly into disturbed areas. *Boerhavia* and *Tribulus* are the most abundant species on the plain, *Eragrostis variabilis* and *Solanum nelsoni* are common, and *Scaevola* is virtually excluded from this area.

Vegetation on Green Island has a definite seasonal growth and reproductive period. This is influenced not only by climatic factors but also to some extent by the vertebrate fauna. Seasonal extremes in precipitation, humidity, temperature, and wind force are not pronounced, yet vegetative growth and flowering occur primarily from June through October. Little vegetative growth and flowering occur in the dominant plant species from November through March. In addition, wind and rain combine during this period to scour and defoliate *Scaevola* growth, primarily on the windward periphery and to a lesser extent elsewhere on the island. This effect is also noticeable in stands of grasses and herbs, especially *Boerhavia,* on the exposed windward dunes and in the central plain. Also during this period albatross excrement, decaying regurgitated food items, and physical trampling have a pronounced deleterious effect on *Sicyos, Boerhavia,* and *Tribulus,* and a lesser effect on *Solanum nelsoni, Eragrostis variabilis,* and *Ipomoea indica,* resulting in reduction of potential food resources for an herbivore and also reduction in the amount of ground cover.

Terrestrial Vertebrate Fauna

In addition to the Polynesian rat, the mammalian fauna of the atoll consists only of the Hawaiian monk seal, *Monachus schauinslandi.* These animals spend much of their time feeding

in the lagoon or lying either on the beach or in the shade of the *Scaevola* at the upper limits of the beach.

Fourteen species of seabirds are known to breed on Kure and 10 migrant or accidental species have been recorded. Wetmore (1925), Kenyon and Rice (1958), Richardson (1957), Robbins (unpublished), Udvardy (1961), Woodside (unpublished), Kepler (1967, 1969), Clapp and Woodward (1968), and Sibley and McFarlane (1968) have presented data on the avifauna of Kure Atoll.

METHODS AND MATERIALS

In September 1963 a study area of 6.94 acres was established on the northwest side of Green Island. The area consisted of 75-percent *Scaevola* community, 22-percent central plain community, and 3-percent dune community, and was considered to be representative of the habitats utilized by the rat. This study plot was gridded at 50-foot intervals to provide a total of 144 trapping stations.

Trapping was conducted for two 4-night periods in October and November 1963 (2,304 trap-nights) and for one 4-night period per month from March 1964 through May 1965 (8,640 trap-nights). Large aluminum Sherman traps were used, one per station, and were left in place during the entire study so that, presumably, they became a familiar part of the environment for animals in the study area. Oat flakes were used throughout as bait. Traps were closed during the day and opened and baited between 1700 and 1900 hours. Animals were marked by a combination of toe and ear clipping. Upon initial capture each month individuals were marked (if necessary), sexed, aged, and weighed. Ectoparasites were identified and the regions in which they were found, together with the extent of their infestation, were noted. Several parameters of reproductive condition were recorded. For males this included condition of the ventral gland (absent, faint, or prominent), size of the scrotum (undeveloped, slightly developed, or fully developed), pigmentation of the scrotum (lacking pigment, slightly, or fully pigmented), condition of testes (undeveloped, slightly, moderately, or fully enlarged), and size of cauda epididymides as determined by swelling of the posterior wall of the scrotum. Reproductive data recorded for females included condition of the vulva (imperforate or perforate), condition of teats (undeveloped, slightly enlarged, or fully enlarged), lactation, and pregnancy as determined by palpation. Subsequent to initial capture each month, only number, age, sex, and trap station were recorded.

Samples were collected monthly from areas adjacent to the trapping area for autopsy. Sample size was 50 from January through November 1964 except for February and March with 39 and 37, respectively, and 25 from December 1964 through August 1965. A total of 757 wild-caught and 106 laboratory-reared known-age individuals were examined. A detailed description of behavior and growth and development of laboratory-reared animals will be presented elsewhere (Wirtz, in press).

The standard measurements of total length, body length, tail length, hind foot length, and length of ear from notch were taken in millimeters and body weights were determined to the nearest 0.1 g. Molt, ectoparasite infestation, and reproductive status were determined externally, and ectoparasites were collected for identification. Weight and measurements of one testis were recorded for males. Tubules of the cauda epididymis were rated as undeveloped, enlarged, or fully enlarged, and tubule smears were examined microscopically for mature sperm. Mammary tissue of females was rated as undeveloped, slightly developed, or fully developed. Condition of the uterus was rated as undeveloped, slightly developed, or fully developed. Numbers of embryos and placental scars and their distribution in the uterine horns were recorded. Resorbing embryos were differentiated in the counts wherever possible. With the aid of a dissecting microscope corpora lutea were counted when present and the maximum diameter of enlarged follicles recorded.

Density and longevity estimates were obtained from a calendar graph of marked animals; and the Hayne (1949*b*) equation, which utilizes the changing role of new to previously handled animals in a given trapping period, was also used to calculate population density estimates from monthly livetrapping data.

Since Christian (1950) suggested that cyclic

declines in mammalian populations might be due to exhaustion of the adrenopituitary system subsequent to the stresses inherent in high population densities, severe climatic conditions, and reproductive activity, numerous workers have reported studies of histological and weight changes in mammalian adrenals that might be correlated with the effects of these stresses. Because of the absence of predators and the possibility that factors inherent in population physiology might play a significant role in the regulation of density in this population, I devoted particular attention to adrenal weight as an indicator of the physiological status of the population. Preserved adrenals were carefully blotted dry and cleaned of fascia before being weighed to the nearest 0.1 mg on a torsion balance. Data were analyzed separately for each sex and age category for which there were sufficient data in order to factor out relationships which were not associated with population density and/or stress.

The subcutaneous and mesenteric fat deposits of all autopsied animals were rated on a subjective scale of one to five, the former indicating no fat deposits and the latter very heavy fat deposits. Indices for the subadult and adult age classes were analyzed to determine the percentage of rats in each group with fat indices for each level of the scale for both subcutaneous and mesentric deposits. Percentages were then multiplied by the index value to weight the observations and the total weighted percentages were divided by 100 to obtain fat indices for both subcutaneous and mesenteric deposits.

The probability of appearance (Davis, 1956), the reciprocal of which is the probability of disappearance, presumably due to death or dispersal, was utilized to obtain an estimate of the survival rate for each age class of the live-trapped population. Dispersal is not believed to be a major factor in the disappearance of animals on a small oceanic island such as Kure. All newly marked animals in each month from October 1963 through December 1964 were considered as separate cohorts, and the sum of individuals surviving at monthly intervals was used to calculate the probability of appearance for each age class.

Calculations of the size of the area utilized by any mammalian species which are based on livetrapping require certain assumptions and contain inherent deficiencies (Sanderson, 1966). It is thus recognized that livetrapping merely provides an estimate of the area which is used by any given individual. For any given species and set of ecological conditions, that extent of the area utilized should be relatively constant. In a population where parameters of population biology change considerably it might be expected that shifts in home range area and extent of movements would reflect these changes. In addition to determining what might be termed a standard home range area for *Rattus exulans* on Kure, livetrapping data were examined for the effects of population density and reproductive activity on the size of the home range.

Detailed analysis of home range area was confined to fertile males and parous females to eliminate possible variability due to age or reproductive status. Three sample periods were established: (1) a period of low density with little reproduction from January through March 1965; (2) one of increasing density and highest rate of reproduction from May through July 1964; and (3) one of high density and no reproduction from September through November 1964. Within each sample period an attempt was made to plot captures for 40 individuals of each sex with three or more nonlinear records. Data were available for 39 males in the January–March sample and only 19 males in the September–November sample.

Minimum home range (Mohr, 1947) was calculated for each individual. Utilization of this method provided determinations of area based only on points within the study area which each individual was known to have visited. In view of recent reports on the movements of small mammals as observed by the use of radioactive tags (Godfrey, 1954; Kaye, 1961), which show that significant areas of the trap-revealed home range may not be utilized, techniques which add area to that minimum determined by trapping do not seem valid for use in estimating home range. The underestimation of home range size because an individual actually ranged farther in one direction than trapping revealed may be balanced by the fact that certain areas within the range of captures may not be utilized. The home range estimate is then an index of the amount of area ranged by a given individual in

order to satisfy its biological requirements, but is not necessarily a measure of the exact physical space in the environment which the animal is using.

Although estimates of home range area provide some index of the space and presumably resource requirements of individuals in the population, techniques for obtaining such estimates are subject to bias introduced by the observer in handling the animals and manipulating the data. An additional means for evaluating the amount of area required by individuals in the population is provided by measuring the distance moved between successive captures. These movements may represent foraging or gametic behavior within the animal's home range or may represent dispersal. Dispersal movements might be assumed to be of greater magnitude, or a pronounced shift in home range location might involve a dispersal movement, but such subjective opinions are difficult to apply with justification to livetrapping data. Movement data, separated into age and sex categories, were utilized in this study as an additional means of examining the interrelationships between density fluctuations, seasonal changes, and reproduction with individual activity.

RESULTS

Age Classes

Juvenile, subadult, and adult age classes are recognized on the basis of weight, reproductive criteria, molt, and chronological age when known (Tables 1, 2, 3). Young animals, less than 4 weeks old and weighing 9 to 25 g constitute the juvenile class. The juvenile pelage differs from that of the adult in that it is softer and finer in texture and lacks the particularly heavy, pale, guard hairs which characterize the adult pelage. All juveniles have undeveloped reproductive tracts.

Animals in postjuvenile molt weighing 20 to 40 g are classed as subadults. This molt begins in rats weighing 20 to 28 g and takes 4 to 5 weeks for completion. None of the individuals in this age class are fertile although some males show slight development of scrotum and testes.

Animals in adult pelage comprise the adult age class. In the wild, animals may live for 18 months or more and in captivity a few individuals have survived for 4 years. Adults may be subdivided into nonbreeding and breeding categories; nonbreeders are characterized by lighter weights and smaller body size; they are younger than breeders, usually less than 8 months old.

In wild females, the vulva may become perforate at weights as low as 40 g and in known-age animals as early as 48 days. However, these newly perforate females show no development of the reproductive tract and are combined with imperforate females of adult weight. Perforation is not definitely indicative of sexual maturity between July and March, as some newly perforate females lack ovarian development. In males the rapid increase in weight is not normally accompanied by maturation of the gonads or accessory sex glands, and these sexually immature animals are also classed as nonbreeding adults. Captive males may become fertile as early as 63 days of age. Enlarged tubules of the cauda epididymides are indicators of mature sperm, and live fertile males can be recognized by the protrusion of the expanded epididymides from the caudal wall of the scrotum. This criterion was utilized to ascertain that males remain fertile throughout the year once sexual maturity is attained.

Body weight is not an absolute basis for age classification. Many rats grow rapidly during the late summer and reach adult weight, but they remain sexually immature. These animals are the nonbreeding adults. There is a decided reduction in population size during the months between November and March. Nonbreeding adults mature sexually in late winter and form, with breeding adults which have survived the winter, the new breeding population. During the winter there are also marked weight losses, and the weight factor is no longer useful for determination of age class. Animals unquestionably in the adult age class on the basis of weight in one month may drop back into the weight group characteristic of subadults in the next month. The concept of calendar age for tagged rats serves no purpose for new animals of low weight. However, from the known limits of the reproductive season at Kure it was possible to assign some animals to the adult class on the basis of minimum age, although their weights were in the range of younger age groups.

TABLE 1

MEAN WEIGHT AND MEASUREMENTS CHARACTERISTIC OF AGE CLASSES ESTABLISHED FOR THE POLYNESIAN RAT OF KURE ATOLL

AGE	SEX	WEIGHT	TOTAL LENGTH	BODY LENGTH	TAIL LENGTH	HIND FOOT	EAR NOTCH	SAMPLE SIZE
Juvenile	Male	17.4 (15.6–19.2)	189 (181–197)	89 (85–93)	100 (96–104)	23.7 (23.0–24.4)	16.6 (15.9–17.3)	21
	Female	14.7 (12.8–16.6)	177 (163–191)	85 (79–91)	92 (83–101)	22.5 (21.3–23.7)	16.0 (14.8–17.2)	11
	All	16.5 (15.1–17.9)	185 (178–192)	88 (85–91)	97 (93–101)	23.3 (22.7–23.9)	16.4 (15.8–17.0)	32
Subadult	Male	29.4 (27.6–30.2)	228 (222–234)	107 (104–110)	118 (111–125)	26.4 (26.0–26.8)	18.6 (18.3–18.9)	40
	Female	27.5 (25.4–29.6)	226 (220–232)	105 (102–108)	121 (118–124)	26.0 (25.6–26.4)	18.5 (18.2–18.8)	40
	All	28.4 (27.0–29.8)	227 (223–231)	106 (104–108)	119 (115–123)	26.2 (25.9–26.5)	18.6 (18.4–18.8)	80
Nonbreeding Adult	Male	53.1 (50.0–56.2)	274 (269–279)	130 (127–133)	147 (140–154)	29.2 (28.9–29.5)	20.0 (19.8–20.2)	40
	Female	41.9 (38.1–45.7)	248 (235–261)	120 (117–123)	135 (132–138)	27.6 (27.3–27.9)	19.7 (19.5–19.9)	40
	All	47.5 (44.8–50.2)	261 (253–269)	125 (123–127)	141 (138–144)	28.4 (28.1–28.7)	19.9 (19.7–20.1)	80
Breeding Adult	Male	75.0 (71.2–78.8)	301 (297–305)	151 (149–153)	151 (148–154)	30.2 (29.9–30.5)	21.3 (21.1–21.5)	40
	Female	62.7 (57.5–67.9)	291 (287–295)	141 (138–144)	150 (148–152)	29.0 (28.7–29.3)	20.9 (20.7–21.1)	40
	All	68.8 (65.3–72.3)	296 (293–299)	146 (144–148)	150 (148–152)	29.6 (29.4–29.8)	21.1 (20.9–21.3)	80

NOTE: 95-percent confidence intervals given in parentheses.

TABLE 2

REPRODUCTIVE CHARACTERISTICS OF MALES BY AGE CLASS, GIVEN AS PERCENTAGE OF SAMPLE SIZE

SAMPLE SIZE AND CONDITION OF REPRODUCTIVE SYSTEM	BREEDING ADULT	NONBREEDING ADULT	SUBADULT	JUVENILE
Sample Size	224	91	94	21
Ventral Gland				
Undeveloped	1.7	95.6	100.0	100.0
Slightly Developed	17.9	3.3		
Fully Developed	80.4	1.2		
Scrotum				
Undeveloped		34.1	77.7	90.5
Slightly Developed		46.2	21.3	9.5
Fully Developed	100.0	19.7	2.0	
Scrotal Pigmentation				
Lacking		1.1		33.3
Slight Deposit		75.8	95.7	66.7
Heavy Deposit	100.0	23.1	4.3	
Testes				
Undeveloped		67.0	97.9	100.0
Slightly Enlarged		23.1	2.1	
Moderately Enlarged	8.9	8.8		
Fully Enlarged	91.1	1.1		
Tubules of Cauda Epididymis				
Undeveloped		95.6	100.0	100.0
Slightly Developed	8.9	4.4		
Fully Developed	91.1			

Reproduction

BREEDING SEASON: Although adult males remain fertile throughout the year, reproductive activity of adult females shows seasonal trends. The occurrence of pregnancy and lactation (Fig. 2) indicates that breeding extends from January through September, with most litters being produced from March through August.

Adult male Polynesian rats have a specialized midventral glandular region (Quay and Tomich, 1963). Because many mammals use glandular secretions to mark territories or as sexual attractants, the size of this glandular region, as indicated by an area of orange secretions and by the intensity of these secretory products, was recorded for adult males (Table 4). Four nonbreeding adults with slightly developed glandular regions were autopsied. Fertile males with fully developed glandular regions were autopsied in every month except September and December; males examined during these months had slightly developed glands. The use of glandular secretions for territorial marking has not been established in this species, though laboratory observations indicate that territorial marking is not its primary function (Egoscue, 1970). The lack of seasonality in the secretions of this gland, as well as in sperm production in breeders, suggests that the time and duration of the reproductive season in this population are somehow regulated by factors of female reproductive physiology. Glandular secretions may serve to attract physiologically receptive females during the reproductive season.

LITTER SIZE: Estimates of litter size were derived from counts of fetuses and placental scars (Table 5). Mean litter size is 3.81 based on fetus counts, with litters of three and four occurring in virtually equal numbers, as compared to a mean of 4.48 calculated from placental scar counts. Mean litter size based on

TABLE 3

REPRODUCTIVE CHARACTERISTICS OF FEMALES BY AGE CLASS, GIVEN AS PERCENTAGE OF SAMPLE SIZE

SAMPLE SIZE AND CONDITION OF REPRODUCTIVE SYSTEM	BREEDING ADULT	NONBREEDING ADULT	SUBADULT	JUVENILE
Sample Size	196	49	72	11
Vulva				
Imperforate		12.3	100.0	100.0
Slightly Perforate	1.5	36.7		
Perforate	98.5	51.0		
Teats				
Undeveloped	22.4	98.0	100.0	100.0
Slightly Developed	44.4	2.0		
Fully Developed	33.2			
Lactating	7.6			
Mammary Tissue				
Undeveloped	56.1	100.0	100.0	100.0
Slightly Developed	9.7			
Fully Developed	34.2			
Condition of Uterus				
Undeveloped	25.5	100.0	100.0	100.0
Slightly Developed	13.8			
Fully Developed	60.7			
Pregnant	62.8			
Corpora Lutea Present	68.9			
Placental Scars Present	48.0			
Enlarged Follicles	39.8			

combined autopsy data is 4.07. Mean size of 59 litters born in captivity is 3.97.

Loss of ova before fertilization or resorption of embryos is among the factors that may reduce litter size in mammals. Resorbing embryos were found in 13 of 123 pregnant females examined. One fetus was affected in 12 females and two in the remaining female. In 52 rats there was an excess of corpora lutea over normal fetuses; in two rats there were more embryos than corpora lutea. The two instances of fewer corpora lutea than fetuses may represent errors in the determination of these structures or the possible occurrence of polyovular follicles. Excesses of corpora lutea are believed to represent either eggs shed and not fertilized or fetuses which failed to develop properly. In seven of the 13 tracts that had resorbing fetuses the number of corpora lutea agreed with that of normal plus resorbing fetuses.

NUMBER OF LITTERS PER YEAR: The relationships between pregnancy and the presence of recent placental scars and enlarged follicles in 183 sexually mature females autopsied during months when reproduction occurred (Table 6) suggest that some females may have two or more litters per season, and livetrapping data support this point. Of the 100 adult females livetrapped in 5 or more months, seven produced two litters in a season and one produced three, while 47 females had only one litter per season. Only one female produced litters in the two successive seasons the population was studied.

FECUNDITY: The observed pregnancy rate on the study area, based on livetrapping data, was 90 litters per season. This represents the production of 360 animals in a breeding season. There were 176 adults handled on the study area in April 1964 when no young were taken. The addition of 360 young to this adult population would have raised the population on the area to about 536 animals by the end of the reproductive season in September if no mortality oc-

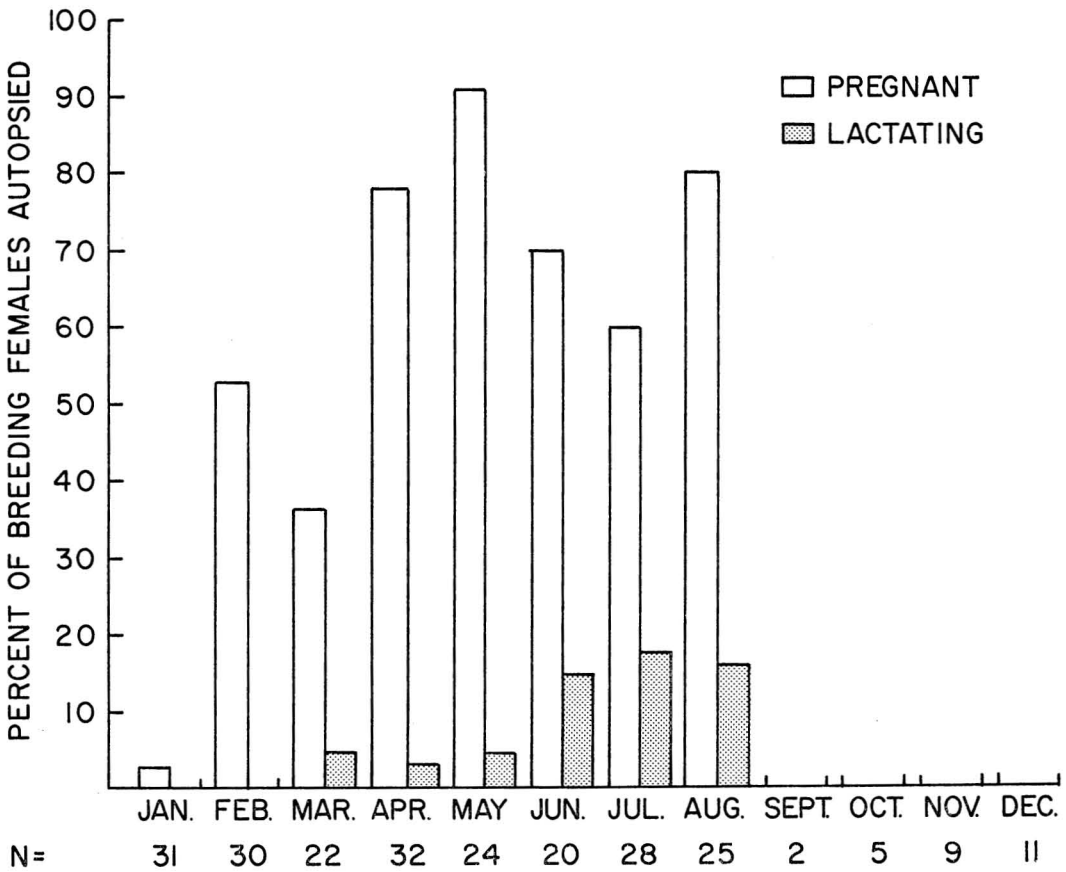


FIG. 2. Occurrence of pregnancy and lactation in breeding adult females, by percentage of females autopsied.

TABLE 4

DEVELOPMENT OF THE VENTRAL GLAND IN FERTILE MALES, BY PERCENTAGE OF AUTOPSY SAMPLE SIZE

MONTH	SAMPLE SIZE	SLIGHTLY DEVELOPED	DEVELOPED FULLY
January	7	42.8	28.6
February	32	31.2	68.8
March	38	7.9	92.1
April	37	10.8	89.2
May	35		100.0
June	19	42.1	57.9
July	24		100.0
August	20	20.0	80.0
September	6	100.0	
October	0		
November	4		100.0
December	2	100.0	

curred. The estimated population of the study area in September was 509 by the Hayne equation and 523 by the calendar graph. The following month the calendar graph indicated a population of 533.

Ectoparasites

The louse *Hoplopleura pacifica* Ewing (= *H. oenomydis* Ferris, 1951) (Haematopinidae) and two mites, *Laelaps nuttali* Hirst and *Laelaps* (= *Echinolaelaps*) *echidninus* Berlese (Laelaptidae), were the only ectoparasites collected on Polynesian rats from Kure. Ticks were present in seabirds' nests on Kure but were not found on rats. No fleas were found on rats. (Frequency of occurrence is based on autopsy data for 757 animals and 3,544 monthly examinations of 1,597 individuals; different in-

TABLE 5

FREQUENCY DISTRIBUTION OF LITTER SIZE BASED ON COUNTS OF PLACENTAL SCARS AND FETUSES IN WILD-CAUGHT RATS AND LITTERS BORN IN CAPTIVITY

LITTER SIZE	FETUSES		SCARS		COMBINED		LITTERS*	
	NUMBER	PERCENT	NUMBER	PERCENT	NUMBER	PERCENT	NUMBER	PERCENT
1	3	2.4	0		3	1.4	0	
2	6	4.8	6	6.9	12	5.7	9	15.3
3	44	35.2	20	23.0	64	30.2	13	22.0
4	45	36.0	20	23.0	65	30.7	16	27.1
5	19	15.2	19	21.9	38	17.9	14	23.7
6	3	2.4	6	6.9	9	4.2	6	10.2
7	4	3.2	4	4.6	8	3.8	1	1.7
8	1	0.8	7	8.0	8	3.8	0	
9	0		0		0		0	
10	0		3	3.4	3	1.4	0	
11	0		2	2.3	2	0.9	0	
Totals	125	100.0	87	100.0	212	100.0	59	100.0

* Born in captivity.

dividuals handled per month varied from 152 to 335.)

The mean frequency of occurrence of *Hoplopleura pacifica* was 94.1 percent (range 74.8–100), with lower values occurring in the warmest and driest months. Young rats seemed more prone to louse infestation. Both adult lice and eggs usually occurred in the fur of the scapular region, perhaps because they are least susceptible to removal by grooming in these regions. The domestic rat mite, *Laelaps nuttalli,* occurred with high frequency ($\bar{x} = 88.4$ percent, range 39.0–99.7) in the population, being more numerous on older animals. Except during March 1964 and February 1965, incidence of this mite ranged between 73.9 and 99.7 percent. The incidence of infestation of the spiny rat mite, *L. echidninus,* was lower ($\bar{x} = 33.0$ percent, range 8.6–64.3) than the other two species. There were normally fewer than a dozen individuals per host. No seasonal trends in degree of infestation were noted, though percentage of occurrence was lowest in May of both years.

TABLE 6

RELATIONSHIP BETWEEN PREGNANCY AND THE PRESENCE OF RECENT PLACENTAL SCARS AND ENLARGED FOLLICLES IN PAROUS FEMALES

CONDITION OF FEMALE	NUMBER	PERCENT
Pregnant with recent placental scars	42	23.0
Pregnant with enlarged follicles	28	15.3
Enlarged follicles and placental scars	31	16.9
Pregnant with both placental scars and enlarged follicles	11	6.0

Food Habits

STOMACH CONTENTS: The diet on Kure is composed of approximately 62-percent plant material and 30-percent insects, while vertebrate flesh accounts for the remaining 8 percent (Fig. 3), based on analysis of a sample of 25 stomachs per month for 1 year. The white berries of *Scaevola* and an occasional entire seed were the only plant items which could be identified in stomachs. Insect remains were most frequent from May through December. Insect families taken included Scarabaeidae, Elateridae (larvae), Noctuidae (larvae), Blattidae, and Formicidae. Vertebrate flesh occurred most frequently in the samples from January, May, June, and December. The winter peaks in consumption of vertebrate flesh occurred when there were few breeding seabirds present, and thus must represent a concentrated effort to obtain this item. The summer peaks of vertebrate flesh consumption occurred when the greatest number of seabirds were breeding at the atoll, and thus probably reflect availability.

OBSERVATIONS AND PREFERENCE TESTS:

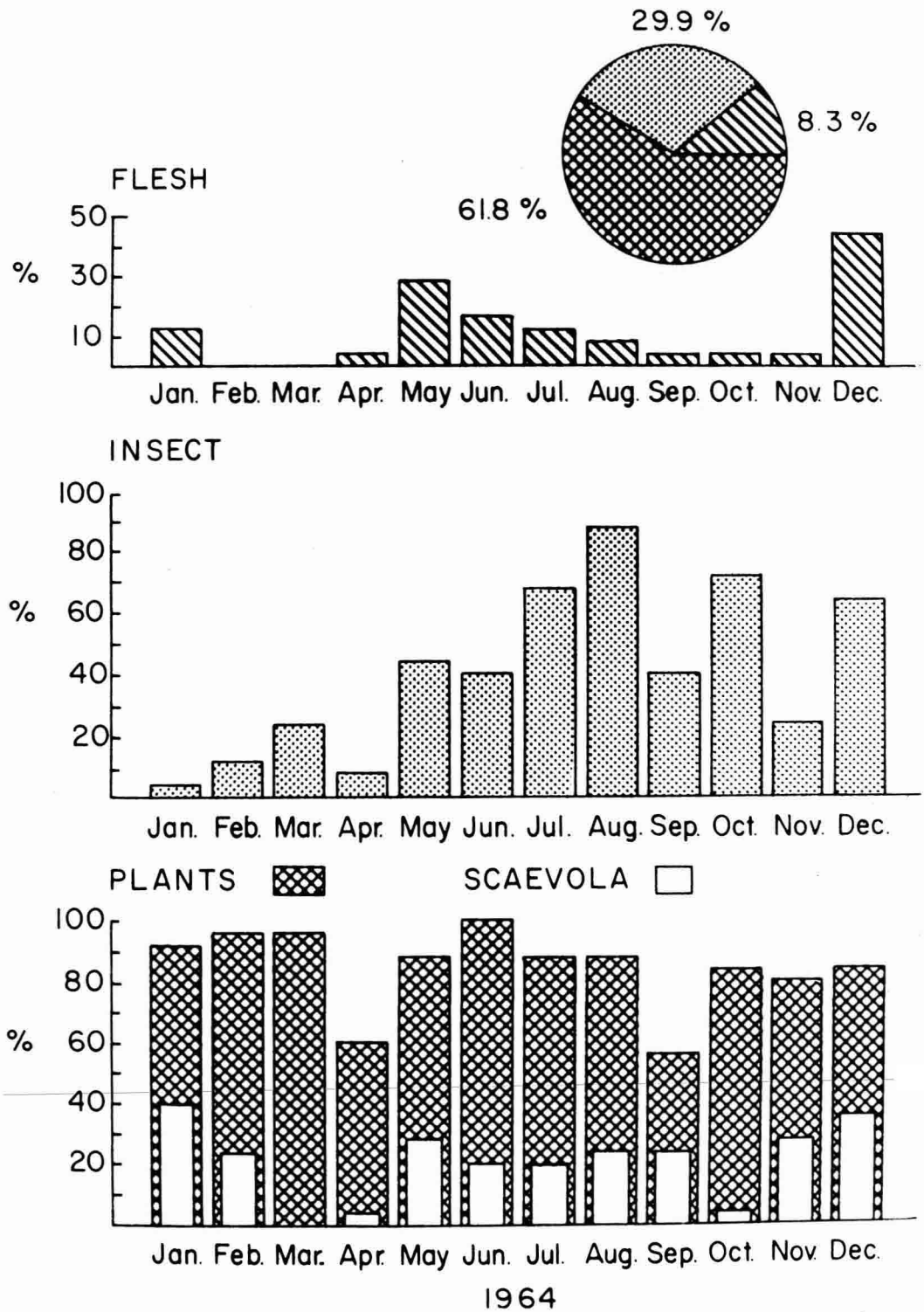


FIG. 3. Frequency of occurrence of major food items based on analyses of stomach contents, and a composite diet for the population on Kure Atoll.

Field observations suggest that the rats rely heavily on the seeds of *Boerhavia diffusa,* the tender shoots and seed heads of *Eragrostis variabilis* and *E. whitneyi,* and the berries of *Scaevola taccada.* Captive rats did not feed on other parts of *Scaevola,* though stems, flowers, and leaves were offered. Captives did not accept parts of any of the other Gramineae recorded on the island. Captive and wild rats fed on the seeds of *Lepidium o-waihiense, Tribulus cistoides,* and *Sicyos hispidus,* but not on the vegetative parts of these plants. Feeding was not noted on any of the introduced plants.

Insects particularly favored by captives were the grasshoppers *Conocephalus saltator* (Tettigoniidae) and *Atractomorpha sinensis* (Acrididae), and the spider *Neoscona vertebrata* (Argiopidae). Roaches (Blattidae) and houseflies (Muscidae) were also taken readily. On several occasions when rat populations were high, animals were observed catching and eating grasshoppers on the lawns of the Coast Guard station.

Although rats were seldom seen on the beaches, they may occasionally feed on regurgitated food items in seal wallows.

PREDATION BY POLYNESIAN RATS: Observations indicate that most species of seabirds on Kure are preyed upon to some degree by rats. Both young and adult of the Laysan albatross, *Diomedea immutabilis,* are killed and eaten (Kepler, 1967). The black-footed albatross, *Diomedea nigripes,* nesting primarily on open beaches where rats do not often venture, does not seem to be attacked.

A high mortality rate was noted among small chicks of the wedge-tailed shearwater, *Puffinus pacificus,* and rats were suspected without conclusive evidence for predation. Rats frequently enter the burrows of this species and those of the Bonin Island petrel, *Pterodroma hypoleuca.* Total destruction of petrel eggs and/or chicks was found in 2 years of this study at the island, though large numbers of eggs were laid in both years. Alsatt (1945), referring to *Rattus rattus* at Midway Island, reported that, "most of the rats live in burrows of the 'small moaning birds' (Bonin Island petrel), and are believed to sustain themselves largely at the expense of that species, including eggs and young," and Walker (in Tomich, 1969) reported Polynesian rat predation on shearwaters and petrels at Kure.

Both eggs and young of the red-tailed tropicbird, *Phaethon rubricauda,* are subject to severe rat damage. The 84 nests in a study area of about 1 acre had an overall chick mortality rate of 64 percent from 31 May to 31 July 1965, with the mortality for the last 2 weeks of July reaching 94 percent. In 1964 about 100 rats were trapped from a semiisolated 2-acre *Scaevola* thicket containing a tropicbird study area before an appreciable decrease in chick mortality was noted. Rats consume offal around the nests of all three species of boobies (*Sula sula, S. leucogaster, S. dactylatra*) at certain seasons of the year; but only one nest failure, that of a brown booby, *S. leucogaster,* was attributed to rat predation during two breeding seasons.

Heavy rat predation on both eggs and chicks of the sooty tern, *Sterna fuscata,* was observed, especially in smaller, isolated colonies of this ground-nesting bird. Rats easily catch and kill small chicks and were observed carrying eggs out of the colonies at night. Predation on small chicks and eggs of the common noddy, *Anous stolidus,* was also noted, especially on chicks which were left unattended shortly after hatching.

Population Dynamics

DENSITY: A total of 1,597 animals was marked. Population density estimates for the 6.94-acre study area are presented in Fig. 4, along with the actual number of different individuals handled each month. Mean monthly density from March 1964 through May 1965 was 45 animals per acre, or an island population of 6,480 rats, with a range of 20 to 75 individuals per acre and a total population fluctuating from 2,880 to 10,800 animals. In late 1963 there were an estimated 50 rats per acre in the study area, or 7,200 on the island. During the period from December 1963 through February 1964 the population declined to an estimated 30 animals per acre, and then increased to a peak of 75 rats per acre following the breeding season. Following this peak, numbers declined to about 20 rats per acre by May 1965. The rate of decline was greatest from November to January when about 30 rats per acre were

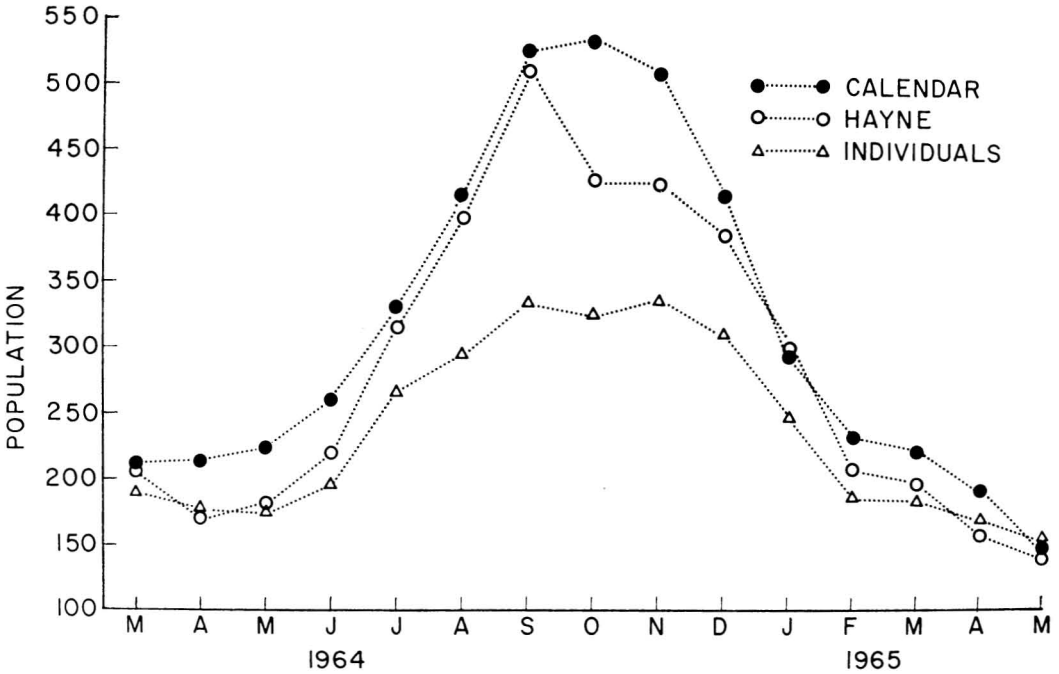


FIG. 4. Population density of rats on the 6.94-acre livetrapping study plot from March 1964 through May 1965.

lost. Total loss from November 1964 to March 1965 was 45 rats per acre, as compared with 26 per acre for the previous year. March density estimates were the same for both years of the study, whereas October–November estimates were different, suggesting that population loss over the winter is density-dependent.

AGE COMPOSITION: Juveniles are first found in the livetrapped population in May (Fig. 5) and are present in low numbers through November. Subadults are first trapped in June and constitute from 12 to 27 percent of the livetrapped population from July through December. Nonbreeding adults form a negligible portion of the population from March through July, then increase to 48 percent of the population by January. Breeding adults comprise nearly 100 percent of the trapped animals in March, April, and May, and are least abundant from September through January.

SEX RATIOS: Thirty-three sets of young which were sexed at birth had a 1:1 sex ratio averaging 1.91 males and 1.94 females per litter. Sex ratios of livetrapped animals varied from 60 to 44 percent males (Fig. 5), although the overall ratio of 50.3 percent males to 49.7 percent females does not differ significantly from the expected 1:1 ratio.

PHYSIOLOGICAL FACTORS: Monthly mean adrenal weights and 95-percent confidence intervals, together with estimated population densities, are presented for subadults, nonbreeding adults, and breeding adults (Fig. 6). No significant differences exist between sexes in any age class. All age classes show fluctuations in mean adrenal weight perhaps due to density, though the response of breeding adults is less distinct than that of other age classes. Pregnancy seems to increase mean adrenal weight in adult breeding females. The mean adrenal weight of pregnant females ($\bar{x} = 30.58$, $s = 9.84$) is 6.36 mg greater than that of nonpregnant but sexually active females ($\bar{x} = 24.22$, $s = 9.77$), a difference that is highly significant ($P \leq .01$).

Monthly mean body weight and 95-percent confidence intervals are presented (Fig. 7) for nonbreeding and breeding adults of both sexes. Nonbreeding adults of both sexes lost from 13

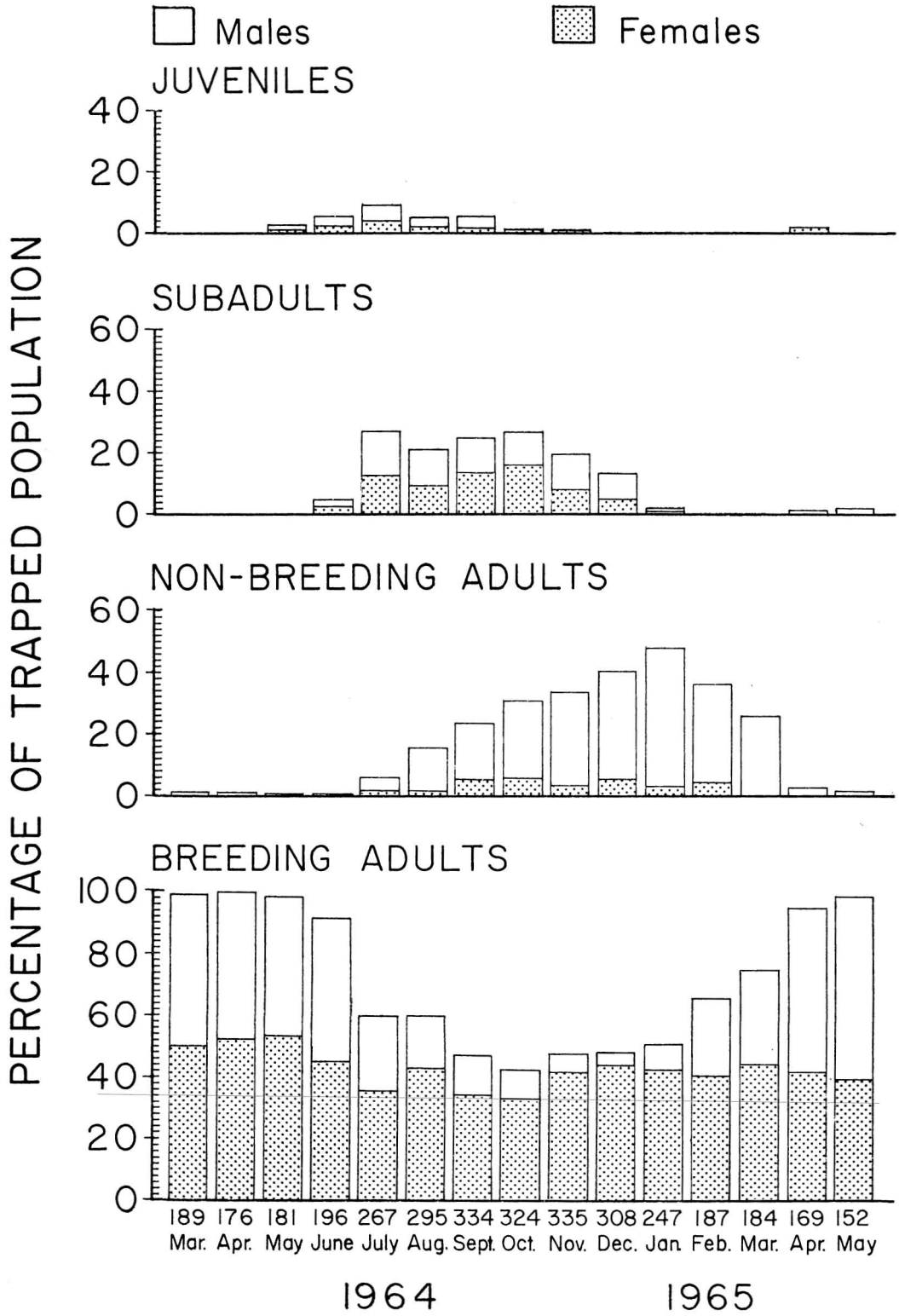


FIG. 5. Age and sex composition of livetrapped rats by month, sample size indicated per month.

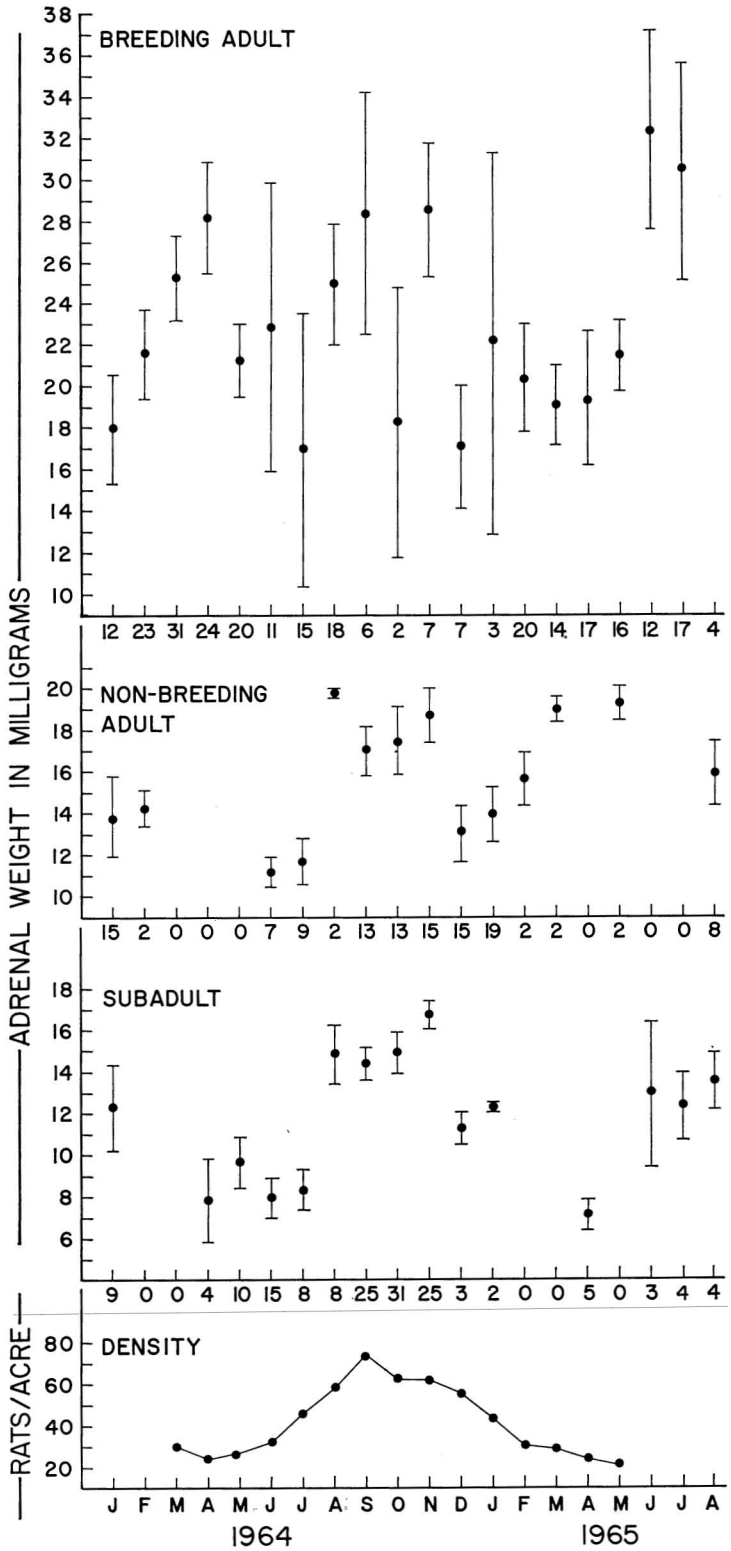


FIG. 6. Monthly mean adrenal weight and 95-percent confidence intervals for all age classes, and population density in rats per acre. Sample size indicated per month.

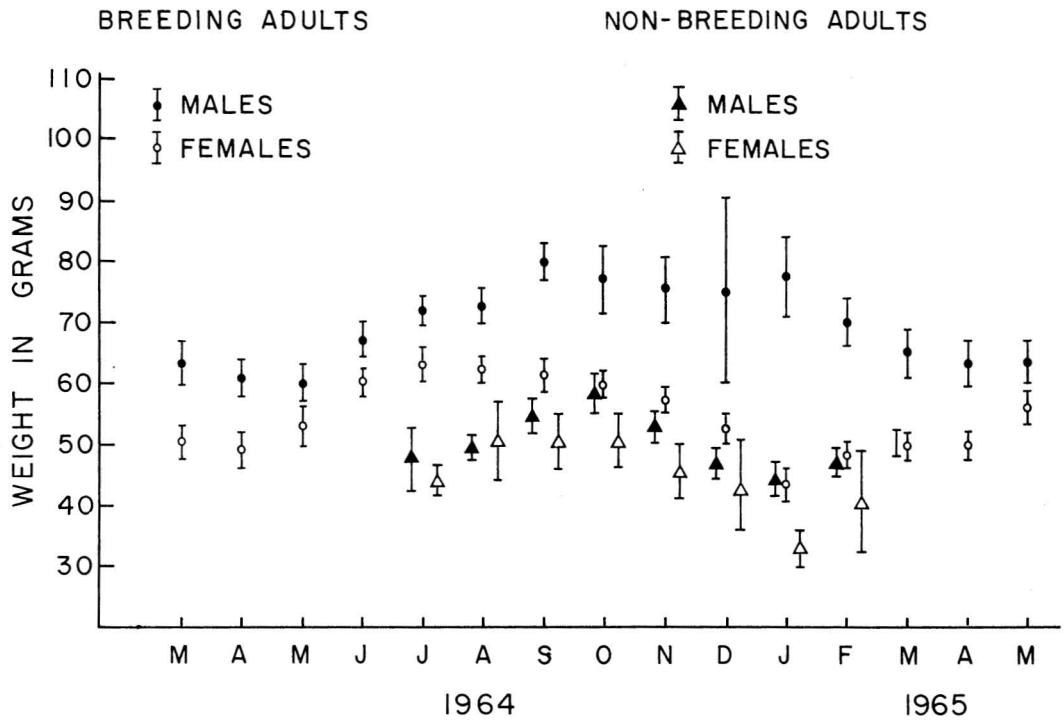


FIG. 7. Monthly mean body weight and 95-percent confidence intervals for adults of both sexes.

to 17 g mean body weight from October 1964 to January 1965. In the same period breeding females lost an average of 19 g mean body weight. Fertile males remained heavy until January 1965, but lost an average of 14 g mean body weight between January and April. Of 183 animals trapped in 4 or more months this winter, 65.6 percent lost weight. Although 50.8 percent of those animals which lost weight disappeared from the trapping records, 49.2 percent of those which did not lose weight also disappeared. Animals which lost weight but survived the winter replaced losses by March or April.

Mesenteric fat deposits were usually less developed than subcutaneous deposits in all age categories (Fig. 8), and subadult deposits were less than adults. Fat is lost from both deposits in late winter, and subadults either had less fat to begin with in the summer months or lost it more rapidly than adults during this period. During winter mesenteric fat was lost at a greater rate than subcutaneous fat in subadults and breeding adults, but at an equal rate to subcutaneous fat in nonbreeding adults. Adult fat deposits increased in April and May, while subadult deposits did not increase until June or July.

LONGEVITY: The "physiological" length of life of Polynesian rats in captivity is at least 4 years. Animals dying after 3 to 4 years have been found to be suffering from nutritional cirrhosis of the liver, nephrosis, and pulmonary edema. Of greater significance is determination of the "ecological" length of life of the species under natural conditions at Kure.

There are no statistically significant differences ($P > .05$) in the probability of appearance between sexes or between breeding and nonbreeding adults, when tested by the standard error of ratios test (Fig. 9). The probability of appearance for animals of both sexes 12 months from initial capture as breeding adults is 0.02. As most rats on Kure do not become sexually mature until after one winter, breeding adults surviving for 1 year after initial capture are living for about 2 years. These data suggest

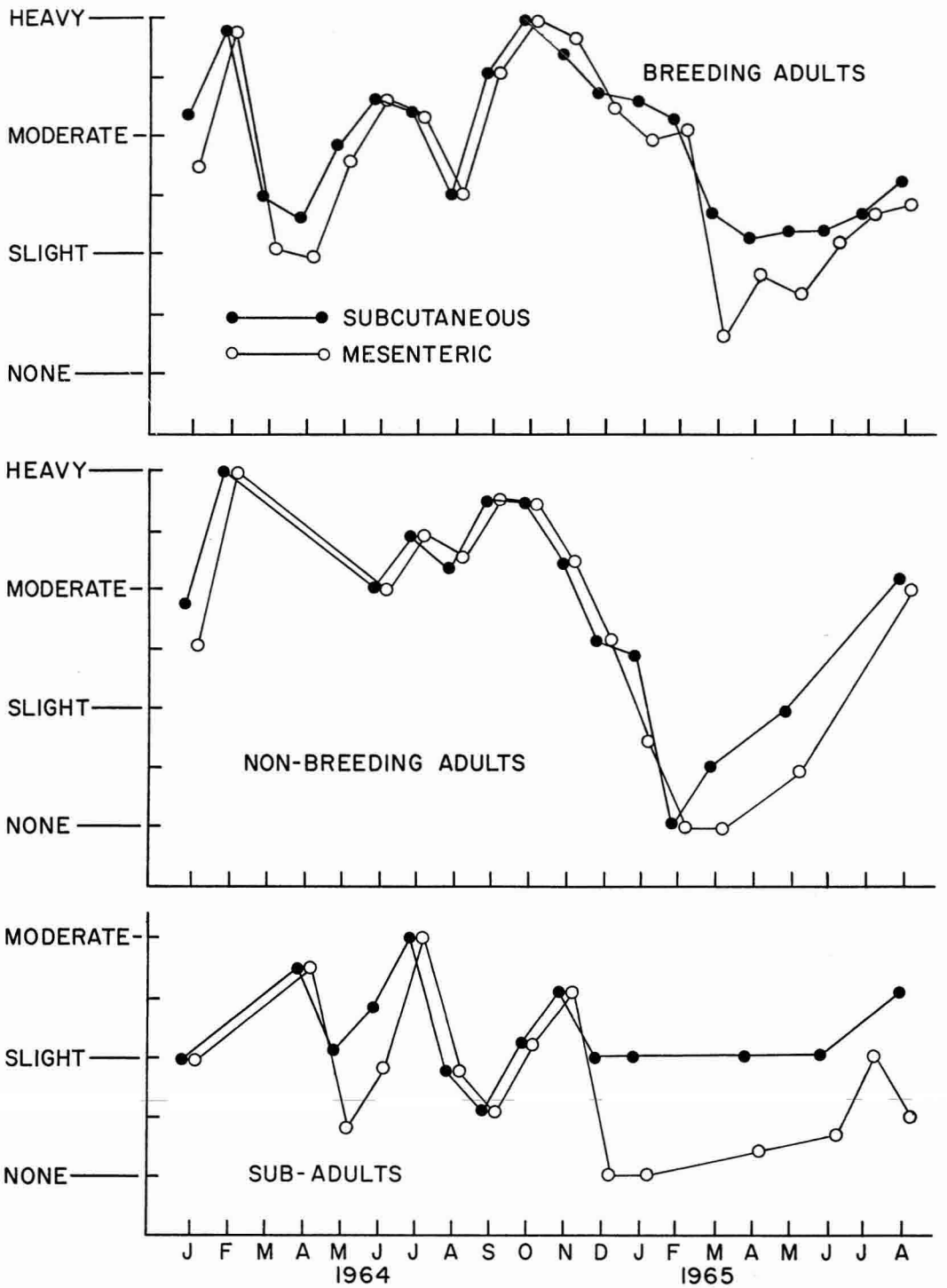


FIG. 8. Seasonal trends in subcutaneous and mesenteric fat deposits in Polynesian rats at Kure Atoll.

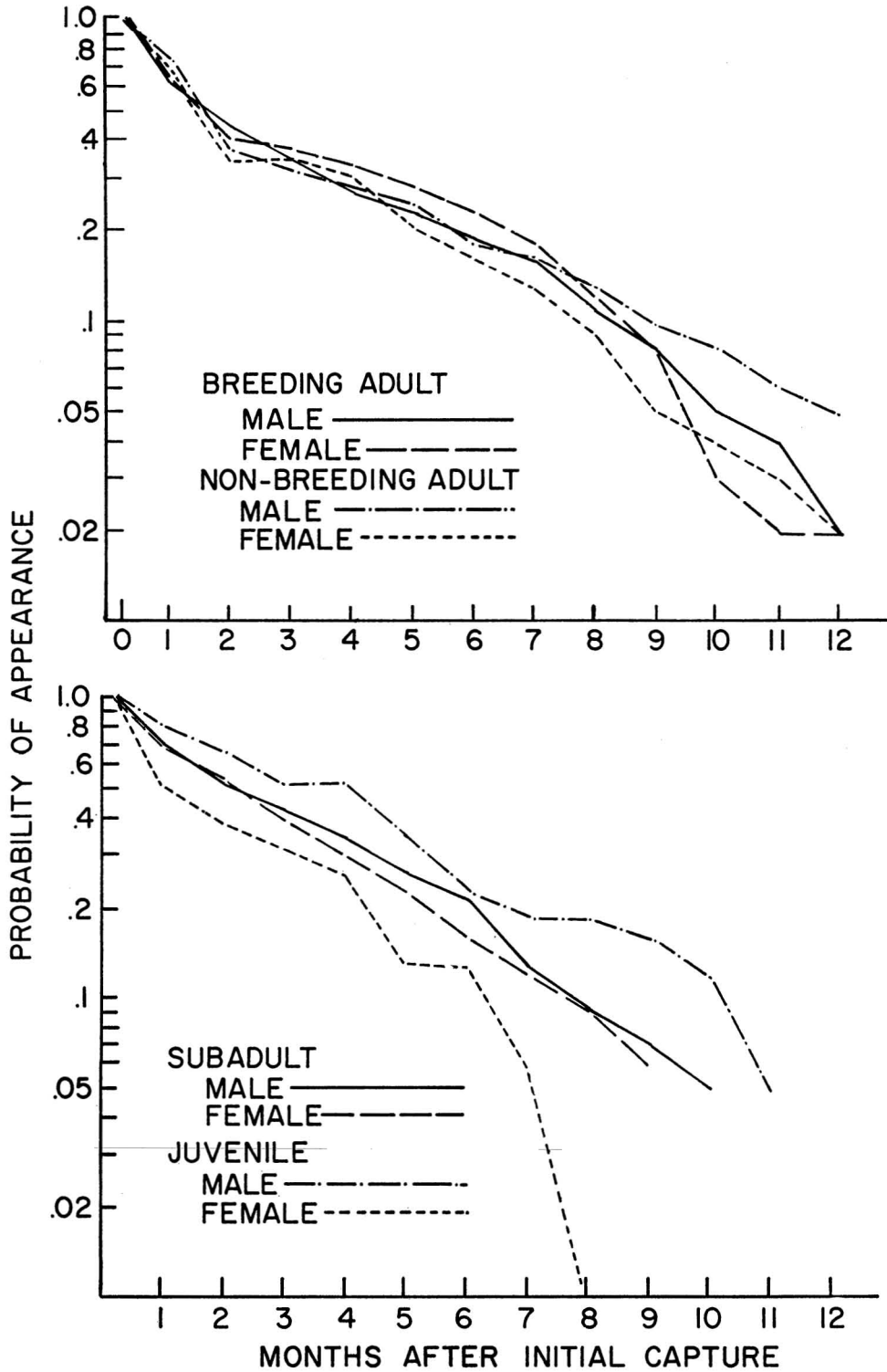


FIG. 9. Probability of appearance for Polynesian rats at Kure Atoll.

that the species on Kure has a mean annual probability of appearance of about 0.45 for adults of both sexes.

No significant differences in the probability of appearance are found between sexes of subadults, but juvenile females are lost at a greater rate than males of this class (Fig. 9). Subadults have approximately the same chance of surviving for 12 months after initial capture as do adults, whereas juvenile females have a poorer chance and juvenile males a slightly improved chance.

Comparative data on seasonal differences in the probability of appearance for adult and subadult age classes (Fig. 10) suggest that animals first taken during late winter or summer survive for longer periods after initial capture than do those first taken during early winter.

MORTALITY FACTORS: Though no mammalian predators of rats are resident on Kure, three species of birds were observed to feed on them on rare occasions. The bristle-thighed curlew, *Numenius tahitiensis,* a regular migrant through the northwestern Hawaiian Islands, was twice observed preying on young rats. In December 1964 two glaucous-winged gulls, *Larus glaucescens,* a species listed as a frequent wanderer to the northwestern Hawaiian Islands (Clapp and Woodward, 1968), regurgitated and voided rat remains when captured alive. It could not be determined from the remains whether the rats had been captured alive or taken as carrion.

The Hawaiian race of the short-eared owl, *Asio flammeus sandwichensis,* is reported to be a rare resident in the northwestern Hawaiian Islands (Bailey, 1956). Individuals were seen on Kure in 9 different months, but did not appear to be resident at the atoll. Castings containing Polynesian rat fur and bones were collected on two occasions, and animals which appeared to be owl kills were seen on several occasions. An injured bird found in February 1964 was fed rats in captivity before it succumbed. However, this specimen has tentatively been identified as the Holarctic form, *Asio flammeus flammeus,* rather than a representative of the Hawaiian race (Clapp and Woodward, 1968).

Dead rats were not commonly observed at the island, though the dense vegetation would preclude frequent observation of carcasses if present. Cannibalism has been observed in captivity, particularly in cases of food or water shortage, but only limited data are available concerning its frequency of occurrence in the wild. On two occasions in November 1964 live rats were observed feeding on rat carcasses. The following month, numerous dead rats were found around the island, and many carcasses had been fed upon by rats, even when they appeared to have been dead for some time.

There is no evidence that disease or parasites played a significant role as mortality factors in the Kure population. Poison is put out irregularly around the Coast Guard station, but is not believed to reach a large percentage of the population, and no program of poisoning or other means of control was conducted elsewhere on the island during the period of this study.

HOME RANGE AND MOVEMENTS: Mean minimum home range was 0.43 acre (0.03 to 1.80) for breeding adult males, and 0.20 acre (0.03 to 1.19) for breeding adult females (Fig. 11), and there was a highly significant ($P \leq .01$) difference between sexes in all sample periods in the mean size of the minimum home range. Mean values for females varied from 34.8 percent to 58.5 percent of the corresponding value for males within the same period.

On the basis of the nonparametric Wilcoxon rank-sum test, no statistical differences in the size of the trap-revealed minimum home range that might be attributed to changes in population density or reproductive activity were detected in the case of either sex.

From the livetrapping data 3,826 measurements were made of the distances moved between successive captures within any month, and the monthly means were examined for effects of density, season, and reproductive activity on the movements of subadults, nonbreeding adults, and breeding adults. With the exception of March 1964 there is a highly significant ($P \leq .01$) difference between sexes of breeding adults in mean monthly distance moved between captures (Fig. 12), and the mean distance between all captures of males (124.6 ft) is significantly greater ($P \leq .01$) than that for females (82.5 ft). Males moved significantly greater ($P \leq .01$) distances between captures

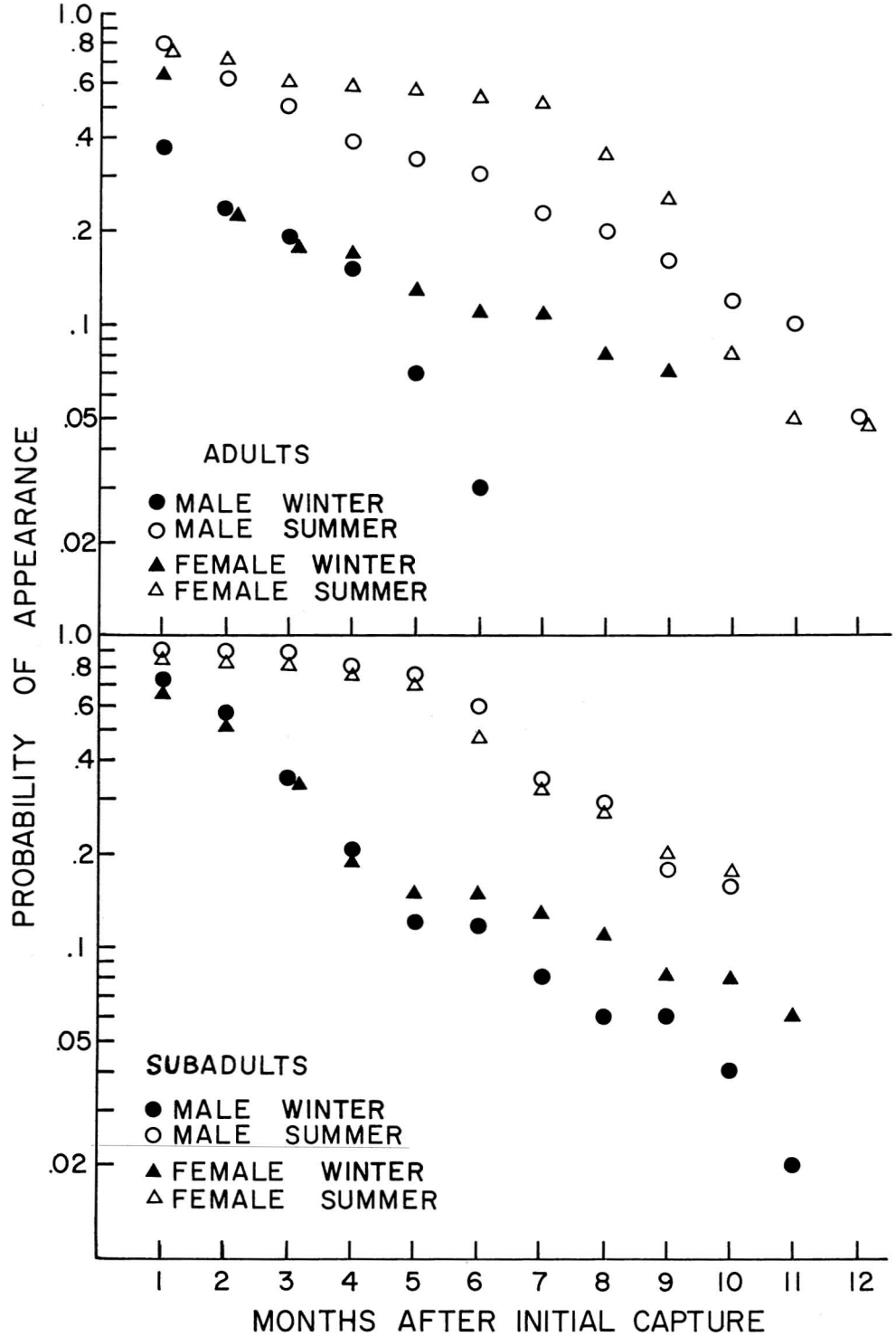


FIG. 10. Seasonal differences in the probability of appearance for subadult and adult age classes at Kure Atoll.

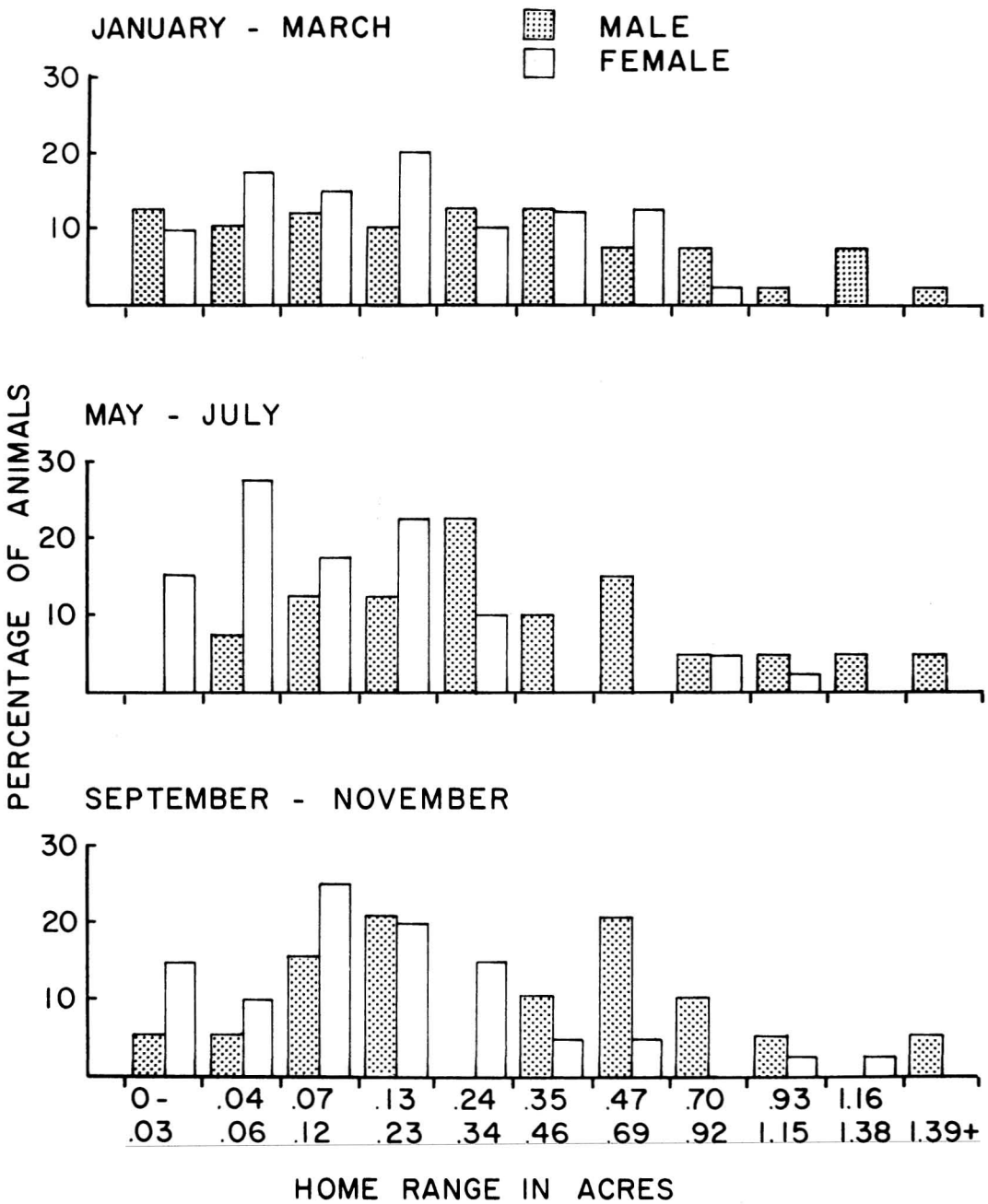


FIG. 11. Frequency distribution of trap-revealed minimum home range of three samples of breeding adults. The January–March period was one of low density with little reproduction; the May–July period, one of increasing density and highest rate of reproduction; and the September–November period, one of high density and no reproduction.

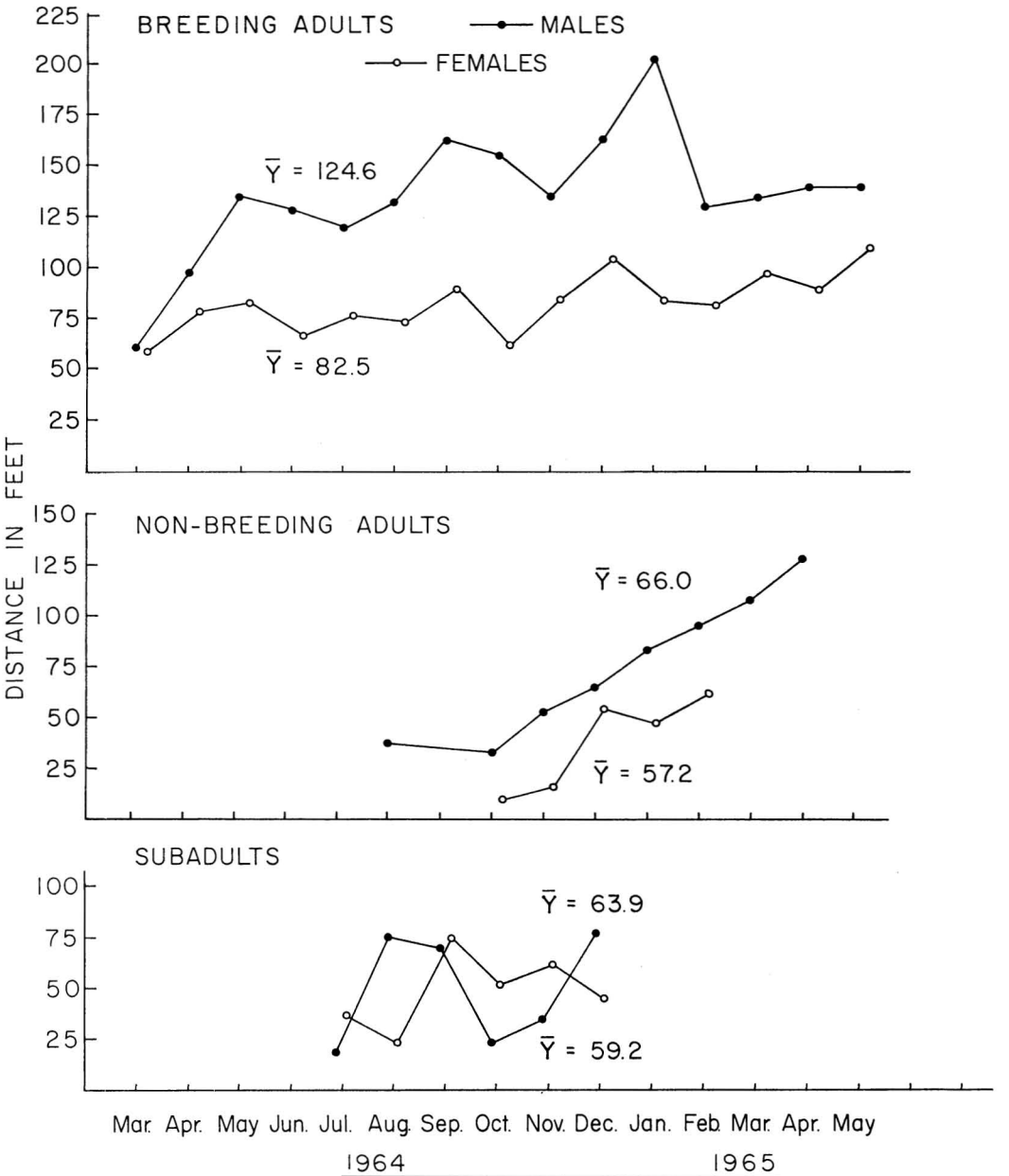


FIG. 12. Monthly mean distance between captures of Polynesian rats at Kure Atoll.

in September 1964 and January 1965 than in the remaining months of the study. Similar, but not significant, trends are noted in the data for females.

No significant difference ($P \geqslant .05$) exists between the mean distance between all captures of nonbreeeding males (66.0 ft) and that for nonbreeding females (57.2 ft) (Fig. 12), although in some months males moved significantly greater distances than females and in 1 month the reverse was true ($P \leq .05$). There was no significant difference ($P \geqslant .05$) in ex-

tent of movement between sexes of subadults (Fig. 12), and monthly mean distances between captures were extremely variable for both sexes.

To measure the extent of movement as related to home range, centers of activity (Hayne, 1949*a*) were calculated for three samples of breeding adults and then superimposed to form a composite map for each sample. Captures were plotted as distances from the computed center of activity and the percentage of captures within 50, 100, 150, 200, and 250 ft from the center of activity were determined for each sample (Fig. 13). The sample periods represented different conditions of density and reproductive activity, the January–March period being one of low density with little reproduction; the May–July period, one of increasing density and highest rate of reproduction; and the September–November period, one of high density and no reproduction. In all samples females exhibited a highly significant ($P \leq .01$) tendency to remain closer to the center of activity than males. There were no significant differences ($P \geq .05$) in the percentage of movement from the center of activity for males between samples. There was a highly significant ($P \leq .01$) concentration of female movements within 100 ft of the center of activity from the January–March sample to the May–July sample, and a significant ($P \leq .05$) increase in movements up to 200 ft from the center of activity from the May–July sample to the September–November sample.

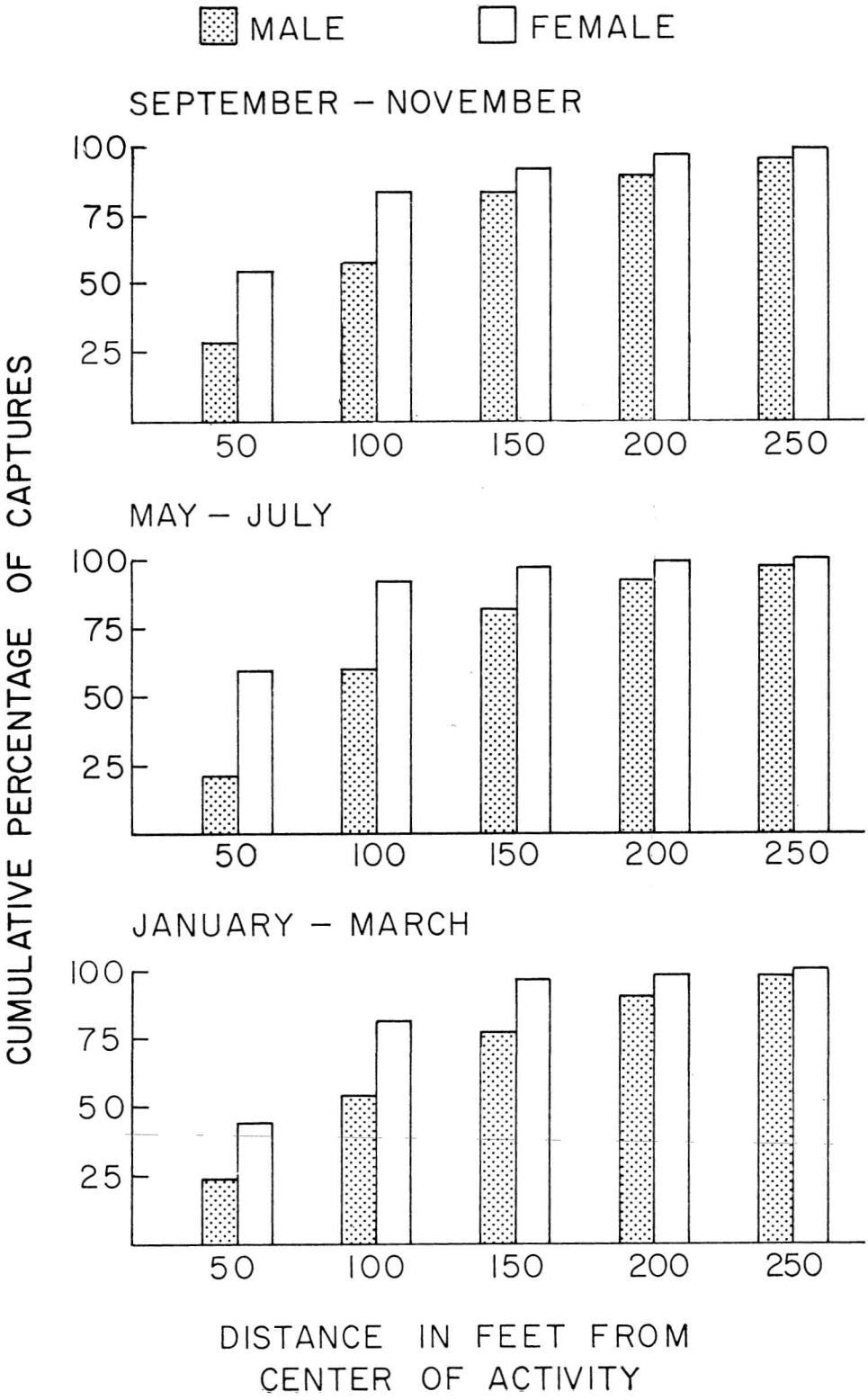
DISCUSSION

The ecological community on Kure Atoll must be considered unique in its stucture, and the information obtained on *Rattus exulans* here is not necessarily expected to agree with that known for the species on larger islands or continental situations, but, rather, is expected to give some indication of the plasticity of the species in its ability to adapt to a variety of ecological situations.

A distinct seasonal breeding period, as found in the Kure population of *Rattus exulans,* seems to be characteristic of the species only in the Hawaiian Islands. Tamarin and Malecha (1971) reported that density of *R. exulans* on Oahu is lowest in summer, followed by increased breeding activity and a cessation of breeding from October through January coinciding with high winter density. Tomich (1970) reported a slight early summer increase of rodents on Hawaii, followed by a great early winter increase and a drastic late winter decrease. Harrison (1952) and Storer (1962) found no evidence of seasonal breeding in Malaya or on Ponape, respectively. Watson (1956) found suggestions of reproductive peaks in the fall in New Zealand, and Nicholson and Warner (1953) noted an increase in reproduction in spring and late summer in New Caledonia, but pregnant females were taken in all months at both localities.

Fecundity is lower on Kure than elsewhere in the range. Malayan females have 4.3 to 4.9 young per litter and 3.2 to eight litters per year, for a mean of 25.7 young per female per year (Harrison, 1951). In a laboratory colony of *R. exulans* from Eniwetok Atoll, Marshall Islands, females averaged 5.2 litters annually with a mean litter size of 3.8 (Egoscue, 1970), for a mean of 19.8 young per female per year. This is very similar to the 18.9 young per female per year reported for Oahu by Tamarin and Malecha (1971). On Ponape only 2.3 to three young are produced per litter, and females bear from one to six litters per year, for a mean of 9.8 young per female per year (Storer, 1962). Litter size averages four on Kure, and females have one or two litters per year, for a mean of about 4.77 young per female per year. The mean annual probability of appearance for the species in Malaya is 0.02 (Harrison, 1956), whereas on Ponape it is 0.40 (Storer, 1962), and on Kure the calculated value is 0.45. A correlation is to be expected between fecundity and survival in these populations. Fecundity is highest in Malaya where annual turnover is greatest, and intermediate fecundities in the main Hawaiian Islands, Eniwetok, and Ponape are associated with reduced survival rates. Low fecundity on Kure may reflect a response of the population, either of genetic origin or mediated through environmental influence, to increased survival as a result of the isolated nature of the population and the absence of mammalian predators.

The single louse species found on Polynesian rats at Kure is the same as that found on rats at Ponape (Storer, 1962). The two mite species


MALE
FEMALE
SEPTEMBER – NOVEMBER
MAY – JULY
JANUARY – MARCH
100
75
50
25
50
100
150
200
250
CUMULATIVE PERCENTAGE OF CAPTURES
DISTANCE IN FEET FROM CENTER OF ACTIVITY

found on rats at Kure are common to the species throughout its range (Elbel and Thaineua, 1957; Ferris, 1932; Marshall, 1955; Storer, 1962). Soft ticks (*Amblyomma* sp.) were taken from *Rattus rattus* on Ponape, but were not found on *R. exulans* (Storer, 1962). Ticks were present in birds' nests on Kure, but were not found on rats. No fleas were found on rats at Kure, though fleas have been reported from *R. exulans* in Honolulu (Cole and Koepke, 1947) and on the island of Hawaii (Haas, 1969; Kartman and Lonergan, 1955*a*).

Throughout its range *Rattus exulans* is predominantly an herbivore. Plant material made up 94 percent of the volume of 46 stomachs examined on Ponape and insect remains were found in 41 percent (Storer, 1962). Baker (1946) noted 80-percent plant materials and 20-percent insect remains in six stomachs from Guam. *Scaevola* and *Tournefortia* made up 78 percent by weight of the diet of *Rattus exulans* on Eniwetok Atoll, whereas insect and animal parts constituted only 2 percent by weight of the diet (Fall, Medina, and Jackson, 1971). *Tournefortia* is rare on Kure, and was not specifically recorded as a food item. Kami (1966) noted that the food of *Rattus exulans* in the main Hawaiian Islands is composed of 67.3-percent by volume sugarcane, 15.1-percent grasses, 6-percent insects, 3.5-percent fruit pulp and seeds, and 8.1-percent animal flesh, earthworms, slugs, nuts, and unidentified material. There are few published reports concerning predation on vertebrates by Polynesian rats in the Hawaiian Islands. Fisher and Baldwin (1946) reported that the Bulwer's petrel, *Bulweria bulweria,* "has been practically wiped out by rats in the last few years" on Popoia Islet off Oahu, and Kepler (1967) describes predation on Laysan albatrosses at Kure. Thoresen (1967) reported that the species takes the eggs of the diving petrel, *Pelecanoides urinatrix,* in New Zealand, and one might assume that predation might occur on other islands where Polynesian rats and nesting seabirds occur together. Polynesian rats do not occur on any other North Pacific island with nesting albatrosses, and *Rattus rattus* at Midway Atoll does not seem to disturb albatross nests though it preys on other species (Alsatt, 1944). Predation and some scavenging constitute the bulk of the relationship between the rat and nesting seabirds at Kure. The period of time during which the community is presumed to have existed suggests that predation on nests and eggs has not been a serious factor in the survival of seabirds at Kure, but quantitative studies are necessary concerning the relationship between predation and seabird productivity at the atoll before any final conclusions can be made.

Responses of monthly mean adrenal weight to population density and to pregnancy in females are suggested for the Kure population, though such relationships were not experimentally verified. Similar responses of adrenal weight to population density have been reported for *Mus musculus* and *Rattus norvegicus* by Christian (1955*a,b*; 1956) and Christian and Davis (1956). These authors also reported continued increases in adrenal weight into periods of population decline. In *Rattus exulans,* however, surviving individuals appear to show a decrease in mean adrenal weight in response to reduction of population density. The data suggest that surviving animals were not as seriously affected by the stresses of high density, and it seems reasonable to propose a graded physiological response among members of the population, with those individuals that are best able to cope with problems of high density and perhaps decreased food and shelter resources being most likely to survive this period. Although decreases in mean body weight during the winter months are also demonstrated for the Kure population, livetrapping data show that the ability to maintain body weight during the winter did not improve an individual's chance for survival, and food availability per se may not be the most important limiting factor in this population.

On Ponape collective data on all age classes suggest that females had a mean annual probability of appearance on two study plots of 0.34; and males, one of 0.19 (Storer, 1962). The authors suggested that the difference between sexes may be attributed to the fact that males at

FIG. 13. Cumulative percentage of captures at various distances from the calculated center of activity of breeding adults at different seasons.

Ponape had larger home ranges and were thus exposed to a greater range of environmental hazards, and that, as a consequence of home range size, females might also live longer than males. Males on Kure were also found to have significantly larger home ranges than females, but this does not appear to have affected their survival rate. Seasonal differences in longevity are demonstrated for the Kure population. It appears that young animals produced later in the breeding season have a poorer chance of surviving the winter and also that older animals that have already survived one winter are not likely to survive a second. This concept is supported by the high loss of breeding adult males in the livetrapped population during the winter months, and these data give further support to the hypothesis that environmental stresses are most severe during the winter months for this population.

As is the case with many small mammals, males had significantly larger home ranges than did females on Kure. In a population where parameters of population biology change considerably during the course of the year it might be expected that shifts in home range area would reflect these changes. Larger home ranges have been associated with lower population densities in *Microtus pennsylvanicus* (Blair, 1940; Linduska, 1942), *Peromyscus leucopus* (Bendell, 1959; Stickel, 1948, 1960), *Peromyscus gossypinus* (Pearson, 1953), and *Zapus hudsonius* (Quimby, 1951). Changes in size of the home range have been reported for the same species in different habitats (Blair, 1951; Layne, 1954; New, 1958), and for the same species in the same habitat but in different years when there were differences in food availability (Layne, 1954; Pearson, 1953). With the large shifts observed in population density on Kure it is perhaps surprising that home range did not respond to density changes. The lack of correlation between home range and density may reflect behavioral or habitat factors. Storer (1962) and Egoscue (1970) reported a high degree of intraspecific tolerance among Polynesian rats on Ponape and in the laboratory. I have made somewhat the same observation except that I have found that fertile males frequently cannot be kept in the same small cage unless they are siblings that have grown up together. Secondly, roughly 90 percent of the habitat on Kure is dominated by dense growths of *Scaevola* with many gnarled, twisted, and intertwined branches. Polynesian rats move freely at all levels in this vegetation so that visualizing the home range as purely two-dimensional may be misleading for this habitat. Rats in the wild may seldom meet, even when home ranges overlap, because of the almost infinite number of paths which the individual might travel; and thus intraspecific stresses may be further minimized. These factors may explain the apparent lack of response in home range area to increased density. Storer (1962), reporting on the home range of *Rattus exulans* on Ponape as calculated by the boundary strip method of Stickel (1954), noted that males moved over larger areas than females; whereas Harrison (1958), using the standard diameter statistic, did not find statistical differences between the sexes in Malaya. The size of home ranges of both sexes was inversely related to population density as measured by trap success on Ponape (Storer, 1962), but these data were for populations in different habitats (rain forest, coconut plantation, grassland) and thus were not directly comparable to the Kure data where home range area was not affected by fluctuations in density in the same habitat.

On Ponape about 70 percent of successive captures of all individuals of this species were within 60 ft of each other (Storer, 1962), and on Guam 77 percent of successive captures were within 75 ft (Baker, 1946). In the main Hawaiian Islands 85 percent of successive captures of individuals taken in and adjacent to cane fields were within 50 ft (Kartman and Lonergan, 1955*b*), although on overgrown mountain slopes only 53 percent of all recaptures were within 100 ft and 81 percent were within 200 ft (Spencer and Davis, 1950). Tomich (1970) reported an average distance between captures of 82 ft for male and 91 ft for female *R. exulans* on Hawaii. Movements of adult Polynesian rats on Kure seem to be greater than those reported for the main Hawaiian Islands. Greater movements on Kure may be related to the uniformity of the habitat and dependence of Polynesian rats on a few species of plants for food, thus necessitating greater foraging effort.

Miller (1958) has suggested that greater movements of adult male *Apodemus sylvaticus*

in England during the reproductive season may be related to the more confining reproductive activities of breeding females. The data presented here for *Rattus exulans* show that the difference in range of movement between adult males and females is not confined to the breeding season and occurs at both high and low population densities, although there is a statistically significant ($P \leq .01$) tendency for breeding adult females to have the smallest range of movement during the May–July period when breeding activity is at its peak. Data for the Polynesian rat on Kure show that most (88.3 to 98.8 percent) captures of both sexes were within 200 ft of the computed center of activity, and virtually all (97.1 to 100 percent) captures of both sexes were within 300 ft of the center of activity. It may thus be assumed that this represents the maximum range of movement for breeding animals with established home ranges, but does not include the occasional sally outside of the range which Burt (1943) excludes as part of the home range.

There is inherent danger in speculating on the seasonality of cyclic density phenomena on the basis of 2 years' data. In the absence of observations on Kure in any years but the 2 studied, the presence of density fluctuations on an annual basis is strongly suggested but not firmly established. Similar fluctuations in density of this species are not suggested by the population data available for Ponape and Malaya (Storer, 1962; Harrison, 1951, 1952, 1955), but are suggested by recent work in the main Hawaiian Islands (Tamarin and Malecha, 1971).

Greater competition from other vertebrates, dispersal, and predation would be among the factors in the more complex mainland and large island ecosystems which could preclude the occurrence of such striking density fluctuations as were observed at Kure.

As the sole terrestrial mammal in this simplified community, the rats face minimum competition with other vertebrates, notably seabirds, and interspecific competition plays little role in species survival. In the absence also of predator pressure one must look for limiting factors solely within the species' biology or biotic environment. As climatic extremes do not exist in this region of the Pacific, it seems unlikely that seasonal weather changes per se would have significant effects on the population's ecology; but several aspects of the data suggest that food availability, fluctuating with the growing season as a result of minor climatic changes, interacts with population density as an important factor in population regulation.

At Kure the winter decline in population density occurs because of the loss of subadult and adult animals when no reproduction occurs and plant food is least available. Conversely the summer increase occurs because of the addition of young from a breeding season during a period in which both plant and vertebrate foods are available. Confined populations of small rodents frequently cease reproduction when densities reach a certain level, and food deficiency frequently results in a marked suppression of reproduction (Christian, 1963). Cessation of reproduction on Kure could be a response either to density or food availability, or to both.

The data obtained on mean body weight and fat deposition suggest that food deprivation does affect the population during the winter. The information presented concerning adrenal weight changes in the population suggest increasing stress factors in the population during periods of high density and also during reproduction in breeding adults. It is not possible from the available information to factor out the specific cause for these increases in mean adrenal weight, but increased gland weights could be a response to density or perhaps to food availability, the latter in turn being affected both by season and rat density. In view of the limited evidence for intraspecific aggression it seems plausible to suggest that the major factor contributing to increased gland weights is the necessity for each animal to work harder for a living during periods of increased density, and the decline in density during the winter suggests that the population has exceeded the available resources. With the loss of large numbers of animals during the winter and the renewal of plant growth in summer population numbers fall within the limits of resources in the absence of predation or noticeable effects of disease.

ACKNOWLEDGMENTS

All field aspects of this study were conducted while the author was employed with the Pacific Ocean Biological Survey Program of the Smith-

sonian Institution. Numerous Survey employees, and especially Robert R. Fleet, Cameron B. Kepler, and Dennis L. Stadel, aided in the collection of data on Kure. Mr. A. Binion Amerson, Jr., of the Survey provided identifications of the ectoparasites.

The author is especially grateful to Lt. Joseph B. Goodwin III, Lt. David A. Worth, and the enlisted men of the United States Coast Guard LORAN station at Kure Atoll for their aid and cooperation throughout the study. Fieldwork in the northwestern Hawaiian Islands was made possible through the cooperation of the Smithsonian Institution, the United States Department of the Interior, the Division of Fish and Game of the Department of Land and Natural Resources of the State of Hawaii, the United States Navy, and the United States Coast Guard.

Laboratory aspects of the study were conducted while the author held a National Institutes of Health Traineeship in the Division of Biological Sciences, Cornell University, with financial support for research from a Grant-in-Aid of Research from the Society of the Sigma Xi, and final rewriting of the manuscript was completed while the author was supported by a Summer Faculty Research Fellowship from Pomona College.

I am sincerely grateful to Dr. James N. Layne for his untiring guidance and stimulating criticism during all aspects of the study. Dr. LaMont C. Cole rendered valuable aid in data analyses, and he and Dr. Howard E. Evans critically reviewed the manuscript. Dr. Larry W. Cohen was very helpful in editing. All figures were done by Merry F. Wirtz, who also helped with laboratory aspects of the research. I am grateful for use of the computer facilities of the Department of Physical Biology, Cornell University (N.I.H. grant FR00326-02).

LITERATURE CITED

ALSATT. R. S. 1945. [Untitled notes on the status of birds of Midway.] Elepaio 5:49–51.

BAILEY, A. M. 1956. Birds of Midway and Laysan islands. Denver Mus. Nat. Hist., Museum Pictorial 12:130.

BAKER, R. H. 1946. A study of rodent populations on Guam, Mariana Islands. Ecol. Monogr. 16:393–408.

BENDELL, J. F. 1959. Food as a control of a population of white-footed mice, *Peromyscus leucopus noveboracensis* (Fischer). Canad. J. Zool. 37:173–209.

BLAIR, W. F. 1940. Home ranges and populations of the meadow vole in southern Michigan. J. Wildlife Mgmt. 4:149–161.

———. 1951. Population structure, social behavior, and environmental relations in a natural population of the beach mouse (*Peromyscus polionotus leucocephalus*). Contr. Lab. Vertebr. Biol. Univ. Mich. 48:1–47.

BLUMENSTOCK, D. I., and S. PRICE. 1967. Climates of the states: Hawaii. Climatography of the United States, no. 60–51. Dep. Commerce, Washington, D.C. 27 p.

BRYAN, W. A. 1915. Natural history of Hawaii. Hawaiian Gazette Co., Honolulu. 576 p.

BURT, W. H. 1943. Territoriality and home range concepts as applied to mammals. J. Mammal. 24:346–352.

CAMERON, J. 1928. John Cameron's odyssey. [Edited by A. Farrell.] New York. 393 p. [Book in Smithsonian Institution library.]

CHRISTIAN, J. J. 1950. The adreno-pituitary system and population cycles in mammals. J. Mammal. 31:247–259.

———. 1955*a*. Effect of population size on the weights of the reproductive organs of white mice. Amer. J. Physiol. 181:477–480.

———. 1955*b*. Effect of population size on the adrenal glands and reproductive organs of male mice in populations of fixed size. Amer. J. Physiol. 182:292–300.

———. 1956. Adrenal and reproductive responses to population size in mice from freely growing populations. Ecology 37:258–273.

———. 1963. Endocrine adaptive mechanisms and the physiologic regulation of population growth. *In*: W. V. Mayer and R. G. Van Gelder (ed.) Physiological mammalogy. Academic Press, New York. 381 p.

CHRISTIAN, J. J., and D. E. DAVIS. 1956. The relationship between adrenal weight and population status of urban Norway rats. J. Mammal. 37:475–486.

CHRISTOPHERSEN, E., and E. L. CAUM. 1931. Vascular plants of the Leeward Islands, Hawaii. Bull. Bishop Mus. 81. 41 p.

CLAPP, R. B., and P. W. WOODWARD. 1968. New records of birds from the Hawaiian Leeward Islands. Proc. U.S. Nat. Mus. 124:1–39.

CLAY, H. F. 1961. Narrative report of botanical

field work on Kure Island, 3 October 1959 to 9 October 1959. Atoll Res. Bull. **78**:1–6.

COLE, L. C., and J. A. KOEPKE. 1947. Problems of interpretation of the data of rodent-ectoparasite surveys, and studies of rodent ectoparasites in Honolulu, T. H., Savannah, Georgia, and Dothan, Alabama. Rep. U.S. Public Health Serv. 202:1–71.

DAVIS, D. E. 1956. Manual for analysis of rodent populations. Edwards Brothers, Ann Arbor, Mich. 82 p.

EGOSCUE, H. J. 1970. A laboratory colony of the Polynesian rat, *Rattus exulans*. J. Mammal. **51**:261–266.

ELBEL, R. E., and M. THAINEUA. 1957. A flea and rodent control program for plague prevention in Thailand. J. Trop. Med. (Hyg.) **6**:280–293.

ELLERMAN, J. R. 1941. The families and genera of living rodents. Vol. 2. Brit. Mus. (Nat. Hist.), Lond. 690 p.

FALL, M. W., A. B. MEDINA, and W. B. JACKSON. 1971. Feeding patterns of *Rattus rattus* and *Rattus exulans* on Eniwetok Atoll, Marshall Islands. J. Mammal. **52**:69–76.

FERRIS, G. F. 1932. Ectoparasites of Marquesan rats, p. 117–127. *In*: Marquesan Insects—I. Bull. Bishop Mus. 98. 244 p.

———. 1951. The sucking lice. Mem. Pacif. Coast Entomol. Soc. **1**:320.

FISHER, H. I., and P. H. BALDWIN. 1946. War and the birds on Midway Atoll. Condor **48**: 3–15.

GODFREY, G. K. 1954. Tracing field voles (*Microtus agrestis*) with a Geiger-Muller counter. Ecology **35**:5–10.

HAAS, G. E. 1969. Quantitative relationships between fleas and rodents in a Hawaiian cane field. Pacif. Sci. **23**:70–82.

HARRISON, J. L. 1951. Reproduction in rats of the subgenus *Rattus*. Proc. Zool. Soc. Lond. **121**:673–694.

———. 1952. Breeding rhythms of Selangor rodents. Bull. Raffles Mus. **24**:109–131.

———. 1955. Data on the reproduction of some Malayan mammals. Proc. Zool. Soc. Lond. **125**:445–460.

———. 1956. Survival rates of Malayan rats. Bull. Raffles Mus. **27**:5–26.

———. 1958. Range of movement of some Malayan rats. J. Mammal. **39**:190–206.

HAYNE, D. W. 1949*a*. Calculation of size of home range. J. Mammal. **30**:1–18.

———. 1949*b*. Two methods for estimating population from trapping records. J. Mammal. **30**:399–411.

JOHNSON, M. S. 1945. Rodent control on Midway Islands. Nav. Med. Bull., Wash. **45**: 384–398.

KAMI, H. T. 1966. Foods of rodents in the Hamakua district, Hawaii. Pacif. Sci. **20**:367–373.

KARTMAN, L., and R. P. LONERGAN. 1955*a*. Wild rodent-flea control in rural areas of an enzootic plague region in Hawaii. Bull. World Hlth. Org. **13**:49–68.

———. 1955*b*. Observations on rats in an enzootic plague region of Hawaii. Publ. Hlth. Rec. **10**:585–593.

KAYE, S. V. 1961. Movements of harvest mice tagged with gold-198. J. Mammal. **42**:323–337.

KENYON, K. W., and D. W. RICE. 1958. Birds of Kure Atoll, Hawaii. Condor **60**:188–190.

KEPLER, C. B. 1967. Polynesian rat predation on nesting Laysan albatrosses and other Pacific seabirds. Auk **84**:426–430.

———. 1969. Breeding biology of the Blue-faced Booby (*Sula dactylatra personata*) on Green Island, Kure Atoll. Publ. Nuttall Ornithol. Club, Cambridge, no. 8. 97 p., 42 tables, 32 fig.

LAMOUREUX, C. H. 1961. Botanical observations on Leeward Hawaiian atolls. I. Notes on the plants of Kure Atoll. Atoll Res. Bull. **69**: 1–10.

LAYNE, J. N. 1954. The biology of the red squirrel, *Tamiasciurus hudsonicus loquax* (Bangs), in central New York. Ecol. Monogr. **24**:227–267.

LINDUSKA, J. P. 1942. Winter rodent populations in field-shocked corn. J. Wildlife Mgmt. **6**:353–363.

MARSHALL, J. T., JR. 1955. Rats of Arno Atoll, Marshall Islands. J. Mammal. **36**:259–263.

MILLER, R. S. 1958. A study of a wood mouse population in Wytham Woods, Berkshire. J. Mammal. **39**:477–493.

MOHR, C. O. 1947. Table of equivalent populations of North American small mammals. Amer. Midl. Nat. **37**:223–249.

MUNTER, W. H. 1915. Annual report of the

Coast Guard for 1915 p. 134–136. U.S. Treasury Dep., Wash.

NEW, J. G. 1958. Dyes for studying the movements of small mammals. J. Mammal. **39:** 416–429.

NICHOLSON, A. J., and D. W. WARNER. 1953. The rodents of New Caledonia. J. Mammal. **34:**168–179.

PEARSON, P. G. 1953. A field study of *Peromyscus* populations in Gulf Hammock, Florida. Ecology **34:**199–207.

QUAY, W. B., and P. Q. TOMICH. 1963. A specialized mid-ventral sebaceous glandular area in *Rattus exulans*. J. Mammal. **44:**537–542.

QUIMBY, D. C. 1951. The life history and ecology of the jumping mouse, *Zapus hudsonius*. Ecol. Monogr. **21:**61–95.

READ, G. H. 1912. The Last Cruise of the Saginaw. Houghton Mifflin Co., New York. 323 p.

RICHARDSON, F. 1957. The breeding cycles of Hawaiian sea birds. Bull. Bish. Mus. 218. 41 p.

SANDERSON, G. C. 1966. The study of mammal movements. A review. J. Wildlife Mgmt. **30:** 215–235.

SIBLEY, F. C., and R. W. MCFARLANE. 1968. Gulls in the Central Pacific. Pacif. Sci. **22:** 314–321.

SPENCER, H. J., and D. E. DAVIS. 1950. Movements and survival of rats in Hawaii. J. Mammal. **31:**154–157.

STICKEL, L. F. 1948. The trap line as a measure of small mammal populations. J. Wildlife Mgmt. **12:**153–161.

———. 1954. A comparison of certain methods of measuring ranges of small mammals. J. Mammal. **35:**1–15.

———. 1960. *Peromyscus* ranges at high and low population densities. J. Mammal. **41:** 433–441.

STOKES, J. F. G. 1917. Notes on the Hawaiian rat. Occ. Pap. Bishop Mus. **3** (4):261–277.

STONE, W. 1917. The Hawaiian rat. Occ. Pap. Bishop Mus. **3** (4):253–260.

STORER, T. I. [*Editor*]. 1962. Pacific island rat ecology. Bull. Bish. Mus. 225. 274 p.

TAMARIN, R. H., and S. R. MALECHA. 1971. The population biology of Hawaiian rodents: demographic parameters. Ecology **52:**383–394.

THORESEN, A. C. 1967. Ecological observations on Stanley and Green islands, Mercury Group. Notornis **14:**182–200.

TOMICH, P. Q. 1969. Mammals in Hawaii. Bish. Mus. Press, Honolulu. 238 p.

———. 1970. Movement patterns of field rodents in Hawaii. Pacif. Sci. **24:**195–234.

UDVARDY, M. D. F. 1961. The Harold J. Coolidge Expedition to Laysan Island, 1961. Elepaio **22:**43–47.

WATSON, J. S. 1956. The present distribution of *Rattus exulans* (Peale) in New Zealand. N.Z. J. Sci. Tech. **37:**560–570.

WETMORE, A. 1925. Bird life among lava rock and coral sand. Nat. Geogr. Mag. **48:**77–108.

WIRTZ, W. O., II. In press. Growth and development of the Polynesian rat, *Rattus exulans*. *J. Mammal.*